AN ABSTRACT OF THE THESIS OF

Carolyn E. Wright for the degree of Master of Science in Botany and Plant Pathology presented on December 7, 1990.

Title: A Systematic and Ecological Study of Astragalus diaphanus (Fabaceae)

Abstract approved: Redacted for Privacy

Kenton L. Chambers

Astragalus diaphanus is a rare plant endemic to the John Day River drainage of north-central Oregon. This species has several interesting features, including the dimorphism of its fruit and its geographical isolation from the two nearest taxonomically related species, which occur in Colorado. This study addressed the species' distribution and habitat, the taxonomic relationships between the varieties of A. diaphanus, certain morphological comparisons among the species, possible reasons for the rarity of A. diaphanus, and the population biology of this taxon.

Astragalus diaphanus was found to be more widespread in the John Day drainage than was previously known, but its range has shrunk due to habitat loss along the Columbia River. In this study, two varieties are recognized within a single species, based on striking morphological differences in pod forms which correspond to a break in geographical

distribution. Other morphological characters are similar between the varieties. Flavonoid analysis and chromosome counts support this taxonomic treatment. Further study is needed to elucidate the relationships of _A. diaphanus_ and its taxonomic relatives in Colorado.

A low reproductive rate in _A. diaphanus_ appears to be a potential problem, possibly contributing to its rarity. The species exhibits a combination of annual and biennial life-cycles. Many annual individuals of _A. diaphanus_ perish without reproducing. This may be off-set by a large seed-bank, which is replenished sporadically by high production in robust biennials.

There is not a need at the present time to provide legal protection to var. _diaphanus_, the more widespread and common taxon. However, var. _diurnus_ has a very limited distribution along the South Fork of the John Day River and is represented by few populations. Many of these are marginally viable, and there are active threats to the existence of the latter variety. _Astragalus diaphanus_ var. _diurnus_ should be afforded legal protection as an endangered species.

A Systematic and Ecological Study of
Astragalus diaphanus (Fabaceae)

by

Carolyn E. Wright

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Typed by researcher for Carolyn E. Wright

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

A SYSTEMATIC AND ECOLOGICAL STUDY OF *ASTRAGALUS DIAPHANUS* (FABACEAE)

INTRODUCTION

The subject of my study is the plant species *Astragalus diaphanus* Douglas ex Hooker, a member of the family Fabaceae, which is endemic to the John Day drainage of north-central Oregon. The species is of interest to taxonomists because of the unusual morphological variability of its fruits, which range in shape from sickle-like and flattened with three angles, to broadly rounded and inflated. Of further interest is the species' isolated geographical occurrence, its two nearest taxonomic relatives being found east and west of the main Rocky Mountain chain in Colorado. *Astragalus diaphanus* has been considered for possible listing as a threatened or endangered species for Oregon.

The purpose of my study was to determine the natural range, habitats, and taxonomic relationships of the races differing in fruit shape within *A. diaphanus*, as well as to compare the taxon morphologically with its two related Colorado species, *A. sparsiflorus* and *A. wetherillii*. I also addressed possible reasons for the rarity of *A. diaphanus* and gathered preliminary data on its population biology.

The study involved field searches for populations of the species, descriptions of its habitats and associated species, and collection of specimens for morphological and flavonoid analyses. Plants were grown in the greenhouse from seeds collected in natural populations. Chromosome counts were made of three of the five taxa in the study. Field studies addressed the annual versus biennial life history strategy of the species, as well as some measures of reproductive success. Finally, threats to the future existence of the species were assessed, to help evaluate its rarity and the need for listing under state and federal endangered species laws.

TAXONOMIC HISTORY

Overview of the Genus

Astragalus L. is one of the largest plant genera in the world, represented by an estimated 1600 species (by some counts up to 3000 species) (Isely 1983). Principal centers of distribution include western North America, the Andes of South America, central Asia, Iran and Turkey (Barneby 1964). It is the largest genus of flowering plants in North America, with about 375 species (Barneby 1989). Within the Fabaceae (Leguminosae), the genus is placed in the subfamily Papilionoideae, the tribe Galegeae (Bronn) Torrey and Gray, and the subtribe Astragalinae (Adans.) Benth. (Polhill and Raven 1981).

An excellent and complete review of *Astragalus* is found in Barneby (1964). The following is a brief summation of that account. The generic name *Astragalus* has a long history in Europe, initially being used for species that possess bilocular pods. A second genus (for which the name *Phaca* was used by Linnaeus and *Astragaloides* by Tournefort) was applied to species with unilocular pods. Both Linnaeus and Tournefort recognized the close relationships between the two genera. This treatment worked well when only a few species were known. However, as botanical explorations in the Old World expanded the knowledge of *Astragalus*, these generic concepts proved difficult to apply. Two botanists, Pallas and DeCandolle, independently produced revisions of Astragalus and related genera at nearly the same time (1800 and 1802, respectively). Pallas rejected Linnaeus' genus Phaca, while DeCandolle recognized three genera: Astragalus, Phaca, and Oxytropis. These works predated most knowledge of New World Astraglus species.

In 1831, Hooker's Flora Boreali-americana treated the North American species of Astragalus and Phaca. This work included several new species described from material provided by Douglas from the Columbia Basin and by Drummond from the Canadian Rocky Mountains and prairies. Hooker followed DeCandolle's interpretation of the genera.

Between 1838 and 1843, Torrey and Gray's Flora of North America was published. It contained about twice as many Astragalus species as had been described by Hooker, based largely on extensive collections by Nuttall. The new species were treated as Astragalus, Phaca, Homalobus, and Kentrophyta. It was becoming evident that the European concepts of Astragalus and Phaca were not compatible with the findings in the New World, although Oxytropis remained distinct and well defined.

Gray, in his 1864 Revision of the North American Species of Astragalus and Oxytropis, proposed that the distinctions between genera no longer be retained for species of the New World. He recognized that Astragalus could indeed be subdivided, but that the resulting new genera would be even less distinct than the existing ones. Instead, Gray recognized a single genus, Astragalus, containing twenty-seven sections which were based on fruit characteristics. Other morphological traits were secondary. Subsequent European classifications followed Gray's definition of Astragalus.

In the 1890's Jones and Rydberg independently began publishing studies on Astragalus. Both eventually completed taxonomic monographs which were extremely different in interpretation of genera and species. Jones was a field botanist, familiar with species in their native settings and aware of natural variations within and between populations. He also addressed phylogeny when creating his sections within the genus. Although most of Jones' species are still recognized today, his phylogenetic concepts have not stood the test of time. Rydberg was a museum botanist who knew plants mostly as dried specimens, but he was very exact and meticulous in his observations. His generic concepts resulted in a fragmenting of Astragalus into twenty-eight genera, a treatment which is no longer accepted.

Barneby began studying Astragalus in the 1940's, combining field and herbarium work. In his 1964 monograph,

Atlas of North American Astragalus, Barneby recognized 552 taxa. His phylogenetic scheme is portrayed by placement of species into small subsections, which are in turn grouped into 93 sections. These are then grouped into seven phalanxes (the general equivalent of subgenera). Oxytropis is treated as a separate genus, following DeCandolle. Isely (1983), in a key to Astragalus species of the United States, generally followed the taxonomic concepts in Barneby's monograph. He differed from Barneby in recognizing Orophaca, a genus originally described by Nuttall, whereas Barneby had treated Orophaca as a well defined phalanx.
There is no current world-wide taxonomic monograph of Astragalus.

Taxonomy and Synonymy of the Species

The publications by Barneby (1964, 1989) and Isely (1983, 1984, 1986) are identical in their placement of the three species studied here. Astragalus diaphanus is a member of subsection Sparsiflori within Section Inflati in the Piptoloboid phalanx. Other species in subsection Sparsiflori are A. wetherillii Jones and A. sparsiflorus Gray.

Astragalus diaphanus was first collected by David Douglas in the 1820's along the south shore of the Columbia River near the Great Falls (presumed to be Celilo Falls). It was described in Hooker's (1831) Flora Boreali-americana.

The specific epithet refers to the translucent pods. It was not recorded again until Joseph Howell and Thomas J. Howell collected it in 1882 along the lower reaches of the John Day River. The latter material was sent to Asa Gray, who published it under the name Astragalus drepanolobus (with sickle-shaped pod) in 1883. At the time, Gray was unfamiliar with Douglas' collection. Jones (1895) placed A. diaphanus as a variety of A. lentiginosus Douglas ex Hooker, with little comment. In 1927 Rydberg discussed both names and voiced the suspicion that A. diaphanus was the oldest name for the species. However, he chose to use Gray's name when he made the combination Hamosa drepanoloba. Barneby (1945) researched the descriptions and type specimens of A. diaphanus, A. drepanolobus, and A. lentiginosus, made the determination that the first two names were taxonomically synonymous, and recognized A. diaphanus as the correct name of a valid species.

Thomas Howell collected the species again in 1885 from the upper reaches of the John Day River near Dayville. His collections were segregated into two sets of specimens, with different names attributed to each. The first set of plants from Dayville constitutes the type collection for A. diurnus, named by Watson in 1886. The name diurnus (i.e. "diurnal") is a pun on John Day. These plants have an inflated pod with scarcely any intrusion of the septum; they were subsequently treated by Rydberg (1929) as Phaca diurna.

Peck (1961), following a suggestion by Barneby, placed the taxon in _A. diaphanus_ under the name _A. diaphanus_ var. _diurnus_. That same year Hitchcock et al. (1961) recognized both _A. diaphanus_ and _A. diurnus_. Barneby (1964) and Isely (1984) no longer recognized the variety, but they suggested that the inflated form is one extreme in a continuum of changes in pod shape which occur along the John Day River. Hitchcock and Cronquist (1973) adopted this interpretation. In agreement with Peck (1961), _A. diaphanus_ is here considered to comprise two varieties, var. _diaphanus_ and var. _diurnus_.

Based on my reconstruction of Howell's travels and my knowledge of _Astragalus_ distribution, the second set of Howell's 1885 specimens was probably collected northwest of Dayville near Picture Gorge. These plants have a slightly inflated pod with a strongly intruded lower septum. Jones found one of these specimens in the herbarium of a "Professor Craig" and named it _A. craigii_ (Jones 1900). It is uncertain whose herbarium Jones was referring to; however, there was a Professor Moses Craig at Oregon Agricultural College, between 1892 and 1897. He began the herbarium and exchanged material to build up the collections. I have located an 1882 Howell specimen in the OSC Herbarium which has a printed label reading "Herbarium of Moses Craig". There is also a sheet at OSC which is probably the holotype collection of _A. craigii_. Its original label, handwritten, reads: "Astragalus drepanolobus, John Day River, Thomas Howell, May 1885". The label data match those with which Jones labeled the fragments he took for his own herbarium. The other sheets of A. craigii were also distributed as A. drepanolobus. Hitchcock et al. (1961) treat A. craigii as a synonym of A. diurnus; however, I consider this taxon to be synonymous with A. diaphanus var. diaphanus.

Astragalus wetherillii was first collected along the Grand River near Grand Junction, Colorado by Alice Eastwood in 1892. It was described by Jones (1893) and is named in honor of Benjamin Alfred Wetherill, an archeological explorer and friend of Alice Eastwood. Rydberg (1905) placed the species in the genus Phaca.

E. Hall and J.P. Harbour collected Astragalus sparsiflorus in 1862 from "On the lower Rocky Mountains of Colorado Territory, about lat. 40°". Two different taxa were collected together, which Gray (1864) described as two varieties. One of these, var. majusculus (rather larger), is a robust form with relatively restricted distribution. A collection of the same taxon at a later date (1894) from Platte Canon was described by Rydberg (1907) as Tium variegatum. Rydberg (1929) later changed his mind about its generic placement and renamed it Batidophaca variegata. The other taxon of Gray, var. sparsiflorus (with scattered flowers), is smaller and more widespread. It was placed in the genus Tragacantha by O. Kuntze. in 1891, then moved to Tium and later to Batidophaca by Rydberg in 1905 and 1929, respectively.

GEOGRAPHIC DISTRIBUTION

Astragalus diaphanus was originally collected along the Oregon shore near the "Great Falls" of the Columbia River in the 1820's. It continued to be seen along the Columbia River from the mouth of the John Day River to Bingen, Washington until the early 1950's, but it apparently became extinct in this area due to inundation by the lakes formed by The Dalles and John Day dams.

The first collections from the John Day River were made in 1882 from near the mouth of the river. In 1885 both varieties were found near Dayville (Grant County) along the upper reaches of the river. Botanists working from 1925 through the 1960's located populations of var. diaphanus near Service Creek and Spray (Wheeler County) and north of Dayville (see Table 1 for information about historical collections). The taxa remained poorly known and rarely collected.

TABLE 1: Historical collections of Astragalus diaphanus.

LOCATION	COLLECTOR	DATE
South side Columbia River	Douglas	unk.
Scot's Bridge, John Day River	J. & T.J. Howell	1882
John Day River near its mouth	T. Howell	1882
John Day River at Dayville	T. Howell	1885
John Day River	T. Howell	1885
Along railroad E of Bingen WA	Suksdorf	1914
Bingen WA railroad	Suksdorf	1920
Squaw Creek, Humphrey's Ranch	Henderson	1925
Columbia River, The Dalles	Peck	1925

TABLE 1 continued

Columbia River 10 mi E The Dalles	Peck	1925
Columbia River 6 mi E The Dalles	Peck	1926
Columbia River 1 mi E The Dalles	Peck	1927
Picture Gorge, NW of Dayville	Ripley & Barneby	1945
John Day River 4 mi SE of Spray	Cronquist	1950
John Day River 2 mi E Service Creek	Hitchcock	1950
John Day River 13 mi W of Spray	Cronquist	1950
Columbia R. mouth of John Day R.	Ripley & Barneby	1951
19 mi S of Fossil	Hitchcock & Muhlick	1962

In 1981, I located a population of var. diurnus along the South Fork of the John Day River south of Dayville. In 1982 Robert Meinke reported populations of var. diaphanus along the North Fork of the John Day River. As part of this study I have located additional populations of var. diurnus along the South Fork of the John Day River, giving the variety a total range of approximately 24 km north-south by 5 km east-west. I have found var. diaphanus in the drainages of the North and Middle Forks of the John Day River and along the main stem and tributaries of the John Day River from Dayville to Clarno. Table 2 presents site data for currently known populations.

TABLE 2: Current locations of *Astragalus diaphanus* by county in Oregon.

LOCATION	LEGAL Tws Rng Sec1/4	*COLLECTOR	DATE
VAR. DIAPHANUS			
Wheeler County:			
Spring Basin, S Clarno	8S 19E 23SE	Wright	1983
17 mi S of Fossil	8S 22E 25SE	*Youtie & Curran	1977
Kahler Basin Road	8S 25E 8NW	*Wright & Gross	1990
1 mi N of Service Creek	9S 23E 7/6	*Wright	1983

TABLE 2 continued

Service Creek	9S	23E	18	*Wright	1983
2 mi E of Service Creek	9S	23E	9NE	Wright & Gross	1990
Juniper Canyon	9S	23E	11NW	*Halvorsen	1984
Hoogie Doogie Mtn area	9S	23E	2	*Youtie & Curran	1977
William Creek	9S	23E	25SE	Halvorsen	1984
Homestead	9S	24E	5	Wright & Gross	1990
Parrish Creek	9S	24E		Wright & Gross	1990
6.5 mi E of Spray	9S	25E	10NW	*Wright	1983
Girds Creek	10S	21E	13/14	Wright & Gross	1985
Morrow County:					
SW of Red Hill	6S	27E	34NE	Urban	1990
Umatilla County:					
NFJDR 4.5 mi E Hwy 395	6S	32E	29SE	Wright & Gross	1984
Grant County:					
Deerborn Creek	6S	31E	29SW	*Meinke	1982
Rd 24, Umatilla NF	7S	27E	23	Urban	1985
Near Devil's Backbone	7S	29E	2	*Meinke	1982
Devil's Backbone	7S	29E	3SE	Wright	1983
Monkey Creek	7S	29E	3SW	Wright & Gross	1984
Wrightman Canyon	7S	29E	17NW	Wright	1983
Three Mile School	7S	29E	27/28	*Wright & Gross	1984
1.5 mi E 3 Mile School	7S	29E	26	Wright	1983
1 mi W Umatilla Co line	7S	30E	3	*Meinke	1982
Buckaroo Creek	7S	30E	4NE	*Wright & Gross	1984
Schoolcraft Creek	7S	30E	4/5	Wright	1983
Eight Mile Creek	8S	29E	1	Wright	1983
Six Mile Creek	8S	29E	10	Wright	1983
E of Ritter, rock pit	8S	30E	14	Wright	1983
6 mi E of Kimberly	9S	26E	14NE	*Wright & Gross	1984
Squaw Creek	11S	25E	30	Wright & Gross	1984
VAR. DIURNUS					
Grant County:					
D-Wave Ranch	13S	26E	13NE	*Wright & Gross	1985
Johnson Creek	13S	26E	24NW	Wright & Gross	1990
Brown Creek	13S	26E	36SW	Wright	1983
Oliver Creek	14S	26E	1NE	Wright & Gross	1984
SFJDR road junction Y	14S	26E	12SW	Wright	1983
N of Jackass Creek	14S	26E	13NW	Wright & Gross	1989
N Magiclantern Creek	15S	26E	24SE	Wright & Gross	1989

Date is most recent year observed.
*Observation only, no collection made.

I have been unable to locate populations along the lower John Day River or the Columbia River. I suspect the species may still occur along the lower John Day River, but access is very difficult. Figure 1 maps all sites reported for *A. diaphanus*.

Astragalus wetherillii occurs principally along the Grand (=Colorado) and lower Gunnison Rivers in Mesa, Montrose, and Garfield Counties, Colorado. Although collected several times, the species is only known from a few locations. It was historically collected from near Moab in Grand County, Utah. A collection in 1979 from Moffat County, Colorado, (*Marv 94* COLO) represents the first time the species has been found outside of the Colorado River drainage.

Astragalus sparsiflorus is found on the Front Range of Colorado. Both its varieties occur in the South Platte River drainage of Denver, Park, and Jefferson Counties. Variety *majusculus* has been collected from relatively few locations, whereas var. *sparsiflorus* is more widespread and its range extends south to the Arkansas River and Pikes Peak area in Fremont and El Paso Counties.

Figure 1. Reported sites of Astragalus diaphanus.

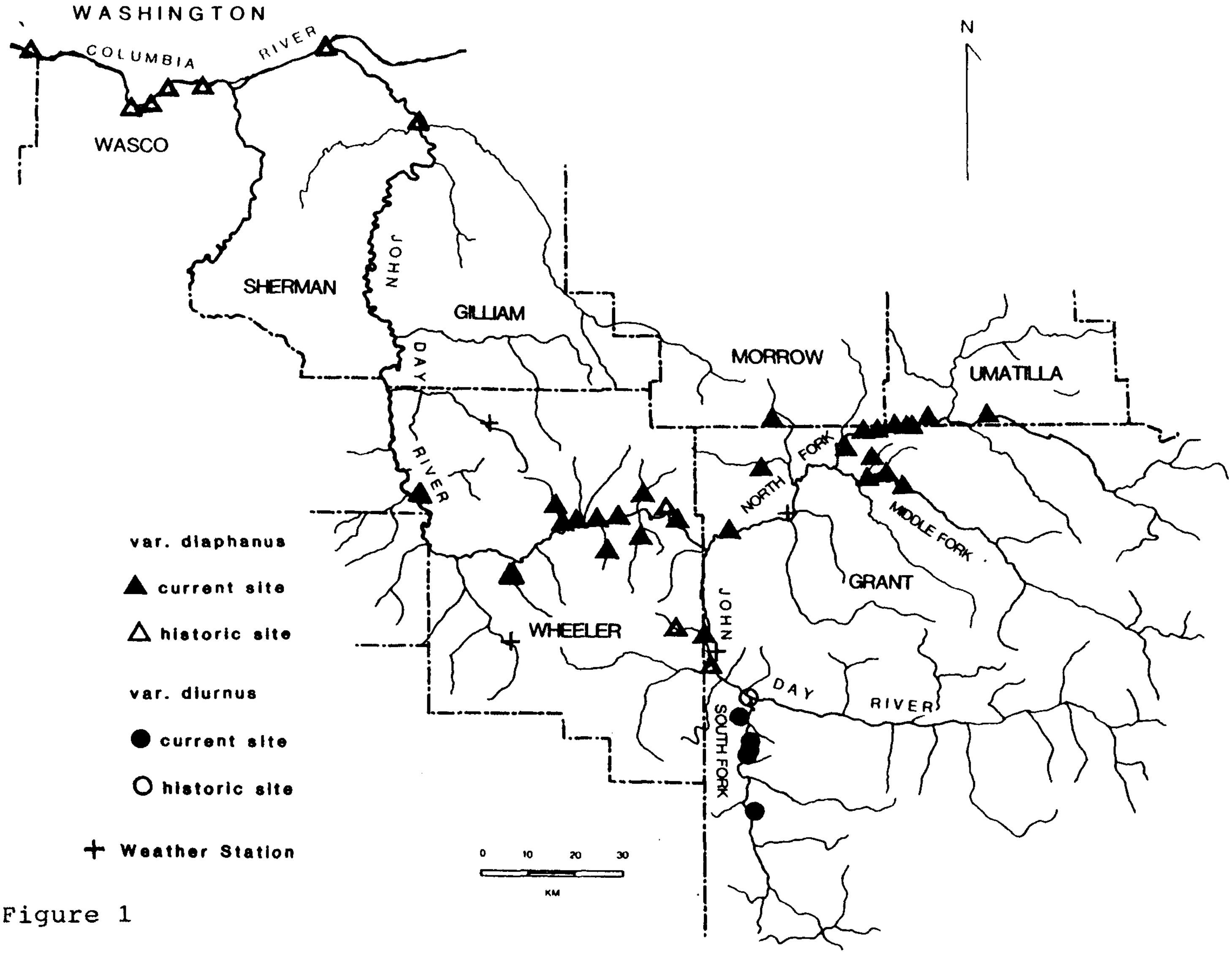

WASHINGTON
COLUMBIA RIVER
WASCO
SHERMAN
GILLIAM
MORROW
UMATILLA
WHEELER
GRANT
JOHN DAY RIVER
NORTH FORK
MIDDLE FORK
SOUTH FORK
N
var. diaphanus
current site
historic site
var. diurnus
current site
historic site
Weather Station
0 10 20 30
KM

Figure 1

HABITAT OF ASTRAGALUS DIAPHANUS

Geology

The information in this section is derived from McKee (1972). The John Day River is a principal drainage in the Blue Mountains Province, carrying water from the western portion of the area north to the Columbia River. The province is elongated east to west, extending from Prineville, Oregon, to western Idaho. It is a highly dissected area providing exposures of a variety of rock strata of many ages. The Blue Mountains area is a large, irregularly shaped anticline bordered on the north by the Columbia Plateau and on the south by the Great Basin. These provinces are characterized by extensive, thick basalt flows of middle to late Miocene age.

Older rocks are exposed in many areas of the John Day drainage. In the upper reaches of the South Fork of the John Day River are Mesozoic strata containing mudstones, siltstones, sandstones and various volcanic deposits. In the region south of Clarno, trending southwest to northeast, are strata dating to the Eocene and Oligocene. These formations include various volcanic flows, tuffs and breccias. Along the John Day River from Picture Gorge to Spray, up the North Fork to Monument and just north and west of Clarno are extensive beds of the John Day formation. This Oligocene to Miocene formation is made up of tuffaceous sandstone and siltstone, welded tuffs and basaltic flows.

All except one population of the currently known stands of A. diaphanus are found on Columbia River basalts. These basalt flows occurred during the middle to late Miocene. While these flows cover many square miles, there are relatively few which border the John Day River. Figure 2 illustrates the distribution of Columbia River basalts along the John Day River and its forks. The basalt is present along the river north of Clarno, from Twickenham to Spray, along the North and Middle Forks above Monument, and along the South Fork. There are sporadic outcrops located with older rock strata. Figure 3 contains photographs showing the basalts near Service Creek along the John Day River and Johnson Creek along the South Fork John Day River.

Overlying the Columbia River basalt flows is the Mascall formation of the late Miocene. It consists of tuff beds and tuffaceous sandstone and siltstone. This formation is located along the John Day River from Picture Gorge to east of Dayville. The Rattlesnake formation of the Pliocene is a welded tuff layer and caps the older strata.

Figure 2. Distribution of Columbia River basalts in the John Day River drainage. (after McKee 1972 and Walker 1977)

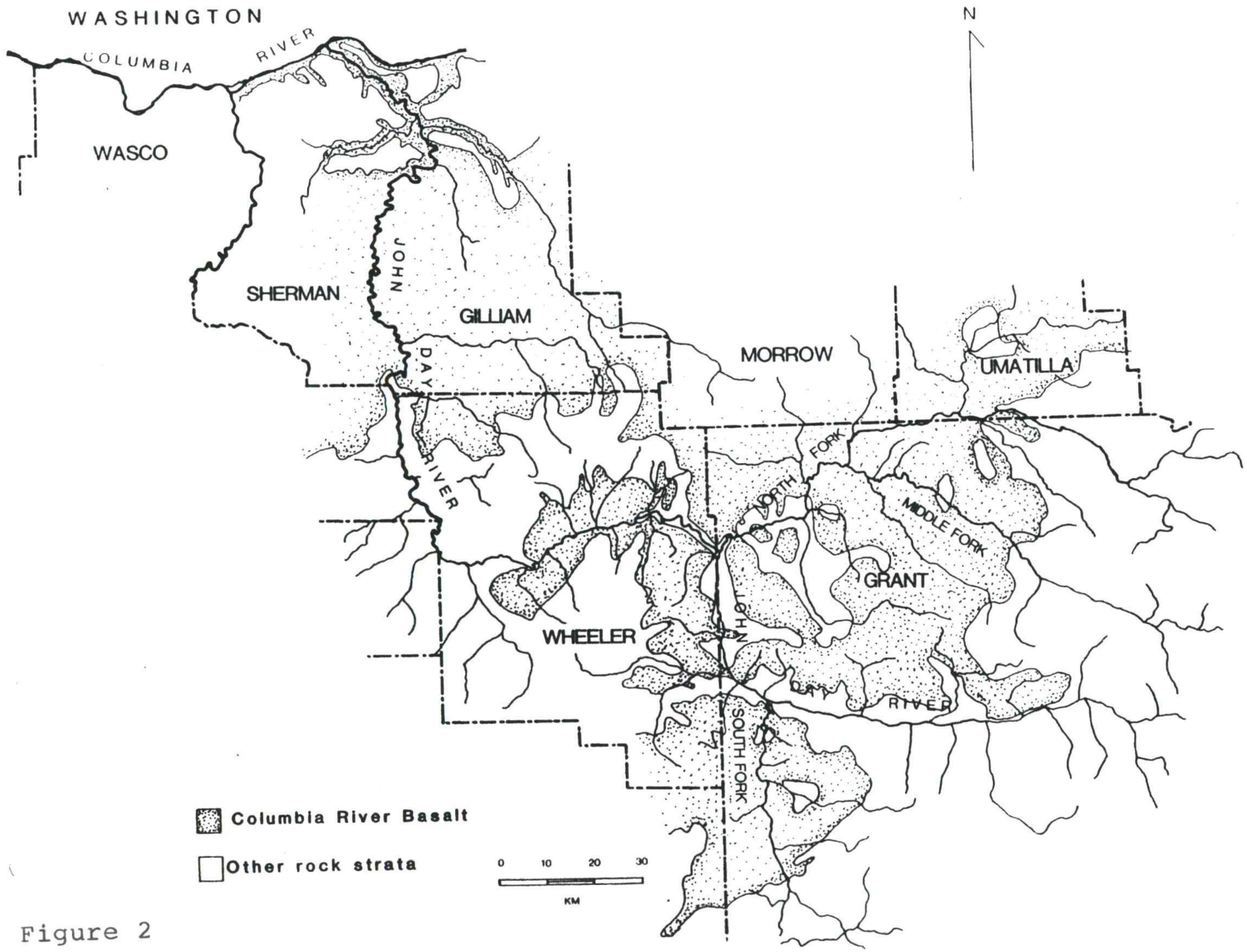

WASHINGTON
COLUMBIA RIVER
WASCO
SHERMAN
GILLIAM
JOHN DAY RIVER
MORROW
UMATILLA
NORTH FORK
MIDDLE FORK
GRANT
WHEELER
JOHN DAY RIVER
SOUTH FORK
N
Columbia River Basalt
Other rock strata
0 10 20 30
KM

Figure 2

Figure 3. Basalts near Service Creek and Johnson Creek. Top: near Service Creek with John Day River in background; bottom: Johnson Creek.

Soils

Materials and Methods

Soils from the site two miles east of Service Creek, and from the Homestead and Johnson Creek sites, were collected in plastic containers and kept refrigerated until tested. Surface samples were collected to the depth of large rocks or bedrock. To determine pH, 10 grams of soil was mixed in 20 ml of distilled water, allowed to sit for one hour, then measured using a pH meter probe. Samples used for the remaining tests were oven dried for 24 hours at 105° C. Soil analyses was conducted by the Oregon State University Soil Testing Laboratory. Phosphorous and total nitrogen were determined by the micro Kjeldahl method using an autoanalyser following digestion. Total carbon was determined by the LECO (dry combustion) method (Page, Miller, & Keeney 1982). Soil classification of the Johnson Creek site was found in the Grant County soil survey (Dyksterhuis 1981). No soil survey has been done in Wheeler County.

Results and Discussion

Soil nutrient levels were extremely low at all sites for each of the elements tested. The pH readings were neutral to slightly basic. Table 3 presents the soil analyses. Total carbon results are not accurate because the machine readings were below the lowest standards available. The Johnson Creek site is classified in the Lickskillet-Rock outcrop complex, with 20 to 70% slopes. In physical appearance, the other locations studied are very similiar to the Johnson Creek site.

TABLE 3: Selected soil characteristics at three sites of *A. diaphanus*.

SITE*	%NH-N	%P	%C	pH
2ESC	0.003	0.055	0.12	7.5-7.6
Homestead	0.003	0.055	0.05	7.0-7.1
Johnson Ck.	0.003	0.093	0.09	7.4-7.5

* Site location data are available in Table 2.

All of the soils analysed were from relatively barren sites with shallow, undeveloped soils. The substrate is basalt. Figure 3 has photographs of two of the localities from which soil samples were taken.

Although low nutrient levels were expected as indicated by the lack of vegetation at the localities, it is interesting to note that the readings were the lowest ever reported in the OSU Soil Testing Lab (Kerl pers. comm.). Nitrogen would probably not be limiting for *Astragalus* due to the plants' root nodulation. The low amount of soil carbon reflects the absence of vegetation at the sites, indicating a lack of organic matter in the soil.

A test for phosphorous (P) availability would have been more useful than the one done for total P. Plants are only able to utilize about one to five percent of the total P present, depending on conditions (Horneck pers. comm.). For this reason it is difficult to know what the level of available phosphorous is at the sites.

Red striping and coloration of leaves and stems may indicate phosphorous deficiencies in plants (Mengel and Kirkby 1982). Astragalus diaphanus is often red-tinged, especially in the fruiting stage of biennial plants. The red coloration is mostly absent during the first spring and fall, then becomes apparent as the plants bolt and age. Plants develop red-margined leaves and red stems as they grow in their second season. The fruits are bright red, and the leaves become entirely red as the plants senesce. Photographs of plants at different ages exhibiting increased red coloration are shown in Figures 4 and 5. Low temperatures and long photoperiods may also enhance anthocyanin production (Moore pers. comm.) Plants at some sites where soil was not tested do not show the same degree of red coloration. Individuals at these sites retain bright green leaves even when fruiting, but may still have red-tinged stems and pods. Plants which were fertilized and grown in the greenhouse did not exhibit any red coloration. This suggests that Astragalus at some locations may experience a phosphorous deficiency. Many of the associated

Figure 4. Seedlings of Astragalus diaphanus in spring and fall with limited red coloration.

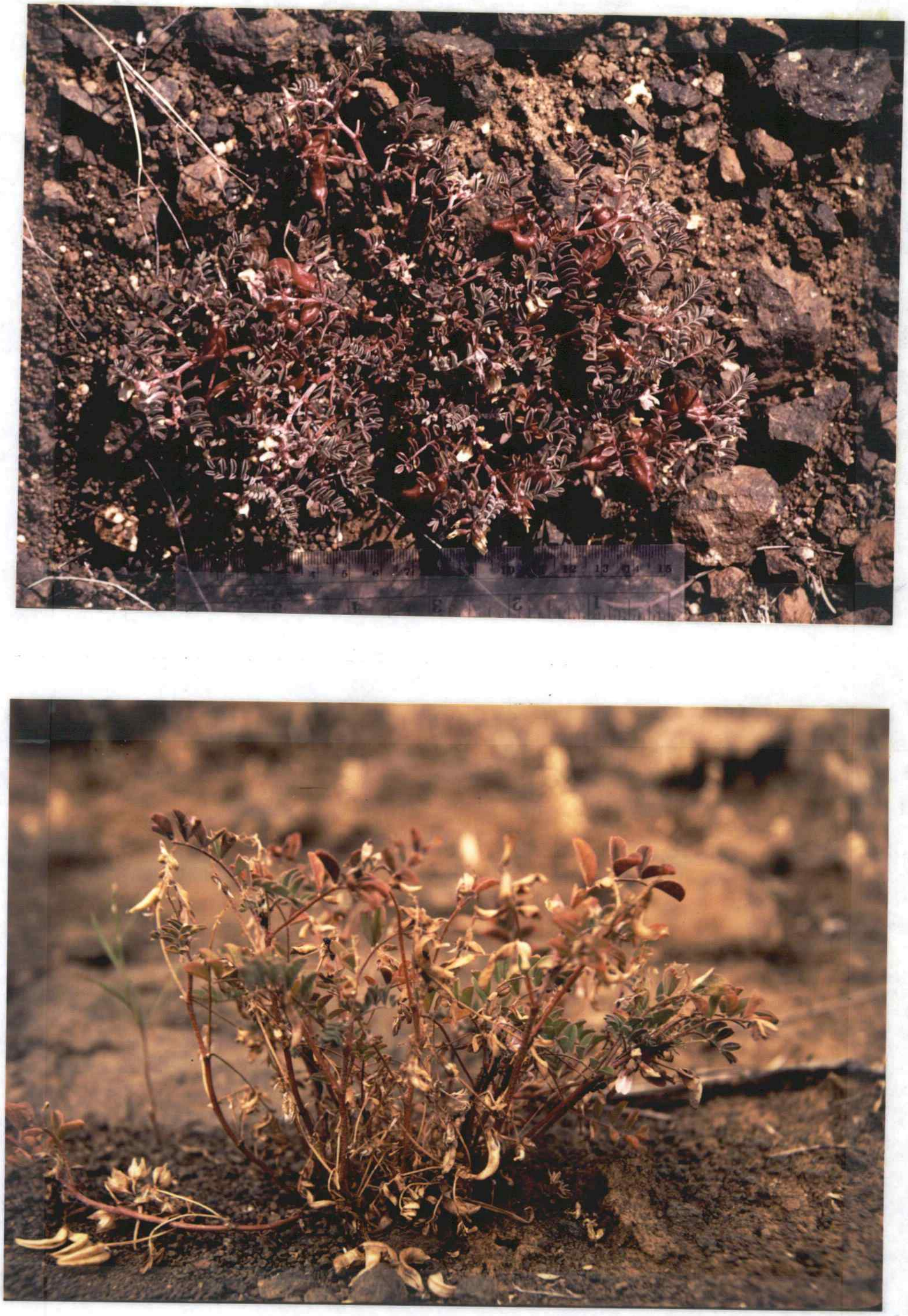


Figure 5. Astragalus diaphanus biennials showing conspicuous red coloration.

perennial species do not exhibit a similiar deficiency, but other annual species do.

Water availability is probably the major limiting factor to growth of the *Astragalus* and other vegetation at the sites. A lack of summer precipitation combined with high runoff and evaporation rates is the probable cause of death for most of the annual *Astragalus* and a cause of death for the biennials. Plants have been observed which appeared to respond to a June rain by a new surge of growth and renewed flowering after the plant was nearly dead.

Climate and Weather

The John Day drainage has a continental climate, characterized by cold winters and warm, dry summers. Precipitation is heaviest in spring and fall, with little falling in July, August, and January. Summer rains are often spotty, while storms at other times of the year are more widespread. Table 4 presents precipitation data by season for selected local weather stations. Winter precipitation may be snow or rain. When I visited sites in the winter along the main stem and South Fork they were always open and free of snow, even when it was snowing on the surrounding hills. I never observed conditions along the North and Middle Forks in the winter. Table 5 presents soil and air temperature readings taken at the three study sites during each visit between September 1984 and May 1985. Data were collected in the afternoon, generally between 12 noon and 3:30 pm.

TABLE 4: Precipitation data for selected weather stations, 1981-1985.

STATION & ELEV.	YEAR	PRECIPITATION IN CM BY SEASON JAN-MAR	APR-JUN	JUL-SEP	OCT-DEC	TOTAL
Dayville	1981	9.22	13.99	3.17	12.47	38.86
685 m	1982	7.47	9.96	7.29	9.78	34.49
	1983	10.34	14.60	4.65	12.04	41.63
	1984	7.24*	14.25	9.78	9.53	40.79*
	1985	3.76	7.06	3.17	6.57	20.57
Fossil	1981	13.64	15.66	6.15	21.77	57.20
803 m	1982	10.95	13.36	9.02	13.72	47.04
	1983	18.06	14.40	5.79	17.75	56.34
	1984	14.32	16.61	4.99	18.39	54.31
	1985	5.08	6.40	6.73	8.84	27.05
Mitchell	1981	9.65	8.31	3.43	12.57	33.96
801 m	1982	4.77	11.38	11.20	7.06	34.42
	1983	9.35	17.15	3.63	14.88	45.01
	1984	7.01	15.98	6.83	13.92	43.74
	1985	4.01	5.89	5.74	8.05	23.69
Monument	1981	13.03	16.59	3.73	16.86	50.21
605 m	1982	10.11	9.96	8.33	12.78	41.17
	1983	18.85	15.98	4.72	14.50	54.05
	1984	14.25	14.78	8.08	12.77	49.88
	1985	5.21	5.89	4.57	8.89	24.56

*One month of data missing.
Taken from National Oceanic and Atmospheric Administration (1981-1985).

TABLE 5: Soil and air temperature measurements taken at three selected locations of *Astragalus diaphanus*.

SITE, ELEV. & DATE	SOIL T* AT 15cm	SOIL T AT 2.5cm	SURFACE TEMP.	AIR TEMP.
2 mi E Service Ck. 515m				
9/7/84	21	24	26	19
9/22/84	19	16	14	12
10/6/84	19	24	24	19
10/26/84	9	9	10	9
11/10/84	11	17	19	16
11/23/84	5	6	7	5
1/19/85	2	8	11	6
2/23/85	8	17	18	12
3/29/85	11	16	16	9
4/26/85	13	19	22	12
5/26/85	33	44	42	27
Homestead 545m				
9/7/84	23	24	26	19
9/22/84	20	12	11	8
10/6/84	21	28	28	19
11/10/84	11	18	18	16
11/23/84	4	6	7	8
1/19/85	1	12	13	6
2/23/85	8	22	24	14
3/29/85	11	20	21	11
4/26/85	16	23	26	14
5/26/85	33	42	37	24
Johnson Creek 810m				
9/7/84	24	30	31	23
9/22/84	17	21	19	12
10/6/84	21	32	31	23
10/26/84	13	14	14	9
11/10/84	8	11	11	11
11/23/84	4	6	8	8
1/19/85	1	7	10	6
2/23/85	9	17	19	13
3/29/85	11	14	13	9
4/26/85	14	20	19	14
5/26/85	27	32	28	23
5/27/85**	19	17	16	13

*Temperature in Centigrade
**Readings taken at 8:10 am.

Associated Species and Plant Communities

Both varieties of *Astragalus diaphanus* occur on relatively barren, rocky sites (see Figure 3). Franklin and Dyrness (1973) classify these communities as lithosolic associations. These particular associations often have a total plant cover of 5% or less. Sites found on the North and Middle Forks of the John Day River tend to be more vegetated, although they remain barren in contrast to the overall community. Surrounding vegetation varies from shrub/steppe types (common along the main stem of the river) to *Juniperus occidentalis* associations and *Pinus ponderosa* associations. Riparian vegetation has been altered by human activities, but is occasionally thick with *Salix*, and along the South Fork particularly, *Populus trichocarpa*, *Rosa* sp., *Clematis* sp., *Alnus* sp. and other common riparian species.

Plant associates were recorded each time a site was visited. Lists of associates are more complete for some populations than for others due to the number of times and months each place was examined. Table 6 lists associated species, compiled from a total of 24 locations. The table is organized with sites along each major branch of the river grouped, so that common associates of that area are more readily apparent. The numbers are percentages of sites along the particular branch that had the given species present.

TABLE 6: Associated species of Astragalus diaphanus var. diaphanus and var. diurnus.

SPECIES*	PERCENT OF SITES WITH SPECIES BY BRANCH OF JOHN DAY RIVER				
(N)	(6)	(4)	(6)	(8)	(24)
Trees and Shrubs	North	Middle	South	Main	Total
Artemisia rigida	0	0	50	25	20.8
Artemisia tridentata	0	0	16.7	25	12.5
Cercocarpus ledifolius	16.7	0	16.7	75	33.3
Chrysothamnus nauseosus	16.7	25	66.7	50	41.7
Eriogonum compositum	66.7	75	33.3	62.5	58.3
Eriogonum microthecum	16.7	0	50	62.5	37.5
Eriogonum sphaerocephalum	16.7	50	16.7	25	25
Gutierrezia sarothrae	0	0	50	87.5	41.7
Haplopappus resinosus	0	0	0	12.5	4.2
Juniperus occidentalis	50	100	83.3	100	83.3
Pinus ponderosa	83.3	50	0	12.5	33.3
Purshia tridentata	66.7	50	66.7	100	70.8
Salvia dorii	0	0	50	50	29.2
Grasses					
Agropyron spicatum	66.7	75	66.7	62.5	66.7
Bromus brizaeformis	50	0	33.3	12.5	25
Bromus mollis	16.7	0	16.7	12.5	12.5
Bromus tectorum	100	100	100	100	100
Poa secunda	100	50	66.7	62.5	70.8
Sitanion hystrix	0	25	0	12.5	8.3
Stipa thurberiana	16.7	50	0	62.5	33.3
Vulpia sp.	16.7	25	16.7	25	20.8
Herbs					
Achillea millefolium	16.7	0	16.7	25	16.7
Allium sp.	0	25	50	0	16.7
Allium macrum	0	0	0	50	16.7
Allium parvum	50	50	16.7	50	41.7
Allium tolmiei	0	50	0	12.5	8.3
Alyssum sp.	83.3	100	83.3	0	58.3
Amsinckia sp.	16.7	25	0	12.5	12.5
Arabis hoelboelii	0	25	0	0	4.2
Astragalus purshii	0	0	33.3	37.5	20.8
Balsamorhiza careyana	0	25	0	0	4.2
Blepharipappus scaber	66.7	50	50	25	41.7
Brodiaea sp.	16.7	50	0	12.5	12.5
Camissonia sp.	0	0	0	12.5	4.2
Castilleja chromosa	0	0	33.3	25	16.7
Chaenactis douglasii	33.3	25	16.7	25	25
Collinsia parviflora	0	25	16.7	25	16.7
Collomia macrocalyx	0	0	16.7	0	4.2
Cryptantha celosioides	50	75	33.3	75	54.2
Cryptantha intermedia	83.3	0	16.7	25	33.3

TABLE 6 continued

Cryptantha sp.	33.3	0	33.3	37.5	29.2
Delphinium sp.	0	0	16.7	25	12.5
Descurainia sp.	0	0	33.3	0	8.4
Draba verna	83.3	25	33.3	50	50
Epilobium sp.	50	50	50	12.5	37.5
Erigeron linearis	16.7	25	16.7	37.5	25
Erigeron sp.	0	50	16.7	25	20.8
Eriogonum strictum	50	25	50	25	37.5
Eriogonum vimineum	0	0	16.7	50	20.8
Eriophyllum lanatum	33.3	25	16.7	25	37.5
Erodium cicutarium	0	50	16.7	37.5	25
Euphorbia serpyllifolia	0	0	0	12.5	4.2
Fritillaria pudica	0	0	0	37.5	12.5
Galium sp.	0	0	0	12.5	4.2
Gilia sp.	0	0	16.7	0	4.2
Holosteum umbellata	16.7	0	50	62.5	37.5
Lesquerella occidentalis	33.3	25	0	75	37.5
Lewisia rediviva	50	25	33.3	37.5	37.5
Lithophragma sp.	16.7	25	50	50	37.5
Lithospermum arvense	16.7	0	0	0	4.2
Lomatium dissectum	16.7	50	16.7	25	25
Lomatium grayi	83.3	100	50	12.5	54.2
Lomatium hendersonii	0	0	33.3	25	16.7
Lomatium macrocarpum	16.7	0	0	0	4.2
Lomatium nudicaule	16.7	0	0	0	4.2
Lupinus lepidus	16.7	0	0	12.5	8.4
Mentzelia laevicaulis	0	0	0	25	8.4
Microsteris gracilis	0	0	0	25	8.4
Mimulus cusickii	0	0	16.7	50	20.8
Mimulus washingtonensis	0	0	16.7	12.5	8.4
Myosotis discolor	33.3	0	0	0	8.4
Orobanche fasciculata	0	0	16.7	12.5	8.4
Pediocactus simpsonii	0	0	0	12.5	4.2
Penstemon deustus	0	25	0	0	4.2
Penstemon richardsonii	0	50	0	25	16.7
Phacelia hastata	66.7	50	16.7	37.5	41.7
Phacelia linearis	0	0	0	12.5	4.2
Plectritis macrocera	33.3	25	16.7	0	16.7
Polygonum sp.	33.3	0	0	12.5	12.5
Potentilla sp.	0	0	0	12.5	4.2
Ranunculus glaberrimus	0	0	0	25	8.4
Ranunculus testiculatus	0	0	33.3	12.5	12.5
Scutellaria sp.	50	25	0	0	16.7
Sedum sp.	0	25	0	0	4.2
Selaginella wallacei	33.3	0	0	50	25
Senecio canus	0	0	16.7	0	4.2
Sisyrinchium sp.	0	25	0	0	4.2
Thysanocarpus curvipes	16.7	0	0	0	4.2
Tragopogon dubius	16.7	0	0	12.5	8.4
Trifolium sp.	0	25	0	0	4.2
moss	50	25	16.7	12.5	25

*Nomenclature follows Hitchcock and Cronquist (1973).

Only my own observations are included; no herbarium label data from other collectors were used.

Habitats along the North and Middle Forks are similiar. The hills above the rivers are generally forested with *Pinus ponderosa* and *Juniperus occidentalis*. Openings occur within the forest where soils are shallow. Some populations are located away from the rivers; however, there is more available habitat along the rivers where there are fewer trees and more rock outcrops. Common associates include *P. ponderosa*, *J. occidentalis*, *Purshia tridentata*, *Eriogonum compositum*, *Agropyron spicatum*, *Poa secunda*, *Bromus tectorum*, *Allium* spp., *Alyssum* sp., *Cryptantha celosiodes*, *Lomatium grayi*, and *Phacelia hastata*.

The South Fork, where var. *diurnus* occurs, is characterized by *Juniperus occidentalis* woodlands interspersed with openings of either shrub/grassland or barren rock outcrops. The canyon is narrow, and the vegetation changes quickly with increased elevation. The upper hills grade into forests of *Pinus ponderosa* and *Pseudotsuga menziesii*. The river is generally more barren to the north with increasing vegetation to the south. Species commonly associated with the *Astragalus* include *Juniperus occidentalis*, *Purshia tridentata*, *Artemisia rigida*, *Chrysothamnus nauseosus*, *Gutierrezia sarothrae*, *Salvia dorrii*, *Eriogonum* spp., *Agropyron spicatum*, *Poa secunda*, *Bromus tectorum*, *Allium* spp., *Alyssum* sp., *Blepharipappus scaber*, *Eriophyllum lanatum*, and *Lomatium* spp.

Sites along the main stem of the John Day River show the greatest variation, probably due to the distances from one section to the next and the variety of aspects encountered. *Juniperus occidentalis* and *Purshia tridentata* were present at all sites. Other common associates include *Cercocarpus ledifolius*, *Chrysothamnus nauseosus*, *Gutierrezia sarothrae*, *Eriogonum* spp., *Salvia dorrii*, *Agropyron spicatum*, *Poa secunda*, *Stipa thurberiana*, *Bromus tectorum*, *Allium* spp., *Cryptantha celosioides*, and *Lesquerella occidentalis*.

MORPHOLOGY

Comparative Species Descriptions

Measurements of twenty-five characters were made on dry, pressed material for *Astragalus diaphanus* var. *diaphanus*, *A. d.* var. *diurnus*, *A. sparsiflorus* var. *sparsiflorus*, *A. s.* var. *majusculus*, and *A. wetherillii*. Specimens examined are listed in the Appendix. Pod drawings were made primarily from pickled or dried, unpressed material.

Astragalus diaphanus var. *diaphanus*: (65 sheets) Annual or biennial, leaves red-margined, stems and pods often red-tinged; finely strigose throughout; tap root slender, fibrous below; branches prostrate, 5-10 (25) cm long in biennials, 1-3 cm in annuals; leaves 2-4 (5.5) cm, petiole 5-20 mm, slightly less than one-half total leaf length; leaflets 7-11 (13), 5-9 (11) by 3-5 (6) mm, elliptic, tips rounded to emarginate, glabrous above, somewhat densely strigose below; stipule triangular, 2-4 mm; peduncle about as long as leaves, raceme 4-12 flowered, pedicels 0.5-1 mm at anthesis, elongating to 1-2 mm in fruit, bract 1-1.5 mm; calyx 2.5-4.5 mm long, the tube 1.5-2.5 mm, the teeth 1-2 mm, the width 1.5-2 mm, corolla white with lavendar veins in the banner, keel purple-tipped, banner 6-9 (10) mm, reflexed, wings 5-8 mm, keel 4-5.5 mm, anthers 0.2-0.3 mm;

pods 14-20 mm long by 3-5 mm wide, overall height 5-12 mm depending on degree of curvature, septum 0.7-1.3 (1.6) mm, pod triquetrous in cross section, incompletely two-celled, lunate, diaphanous, ovules 10-14, seeds light brown to black, 2-2.4 mm long by 1.6-1.8 mm wide; pods open from distal end, deciduous, pedicels persistent on stem, gynophore of 0.5 mm rarely present. Illustrations of pods are in Figure 6.

Astragalus diaphanus var. *diurnus*: (15 sheets) Annual or biennial, stems and pods often red-tinged, leaves red-margined; plant strigose throughout; branches prostrate, 10-20 cm long in biennials, 1-3 cm in annuals; leaves 3-5.5 cm with petioles 10-20 (25) mm long; leaflets (7) 9-11, 6-9 (11.5) mm long by 3-5.5 mm wide; stipules 2-3 mm; peduncles about as long as leaves, racemes 5-8 (12) flowered, flowers erect, becoming lax with age; pedicel 0.5-1 mm at anthesis, elongating to 1.5-2 mm in fruit, persistent on stem; calyx 3-4.5 mm, the tube (1.5) 1.7-2.3 mm long by (1.5) 1.7-1.9 (2.5) mm wide, with teeth (1) 1.5-2.2 mm; corolla white with lavendar lines in the banner and the keel purple-tipped, banner 6.5-7.5 (9) mm, reflexed, wings (5) 5.5-6.5 (8) mm, keel 4-4.5 (5.5) mm, anthers 0.3 mm; pod 17-20 (25) mm long by 8-10 (12) mm wide, septum at base of pod (0.2) 0.3-0.4 mm, pod inflated, round in cross-section, one-celled, opening from distal end, deciduous, seeds light brown to black, 2.4-2.7 mm long by 1.8-2.2 mm wide;

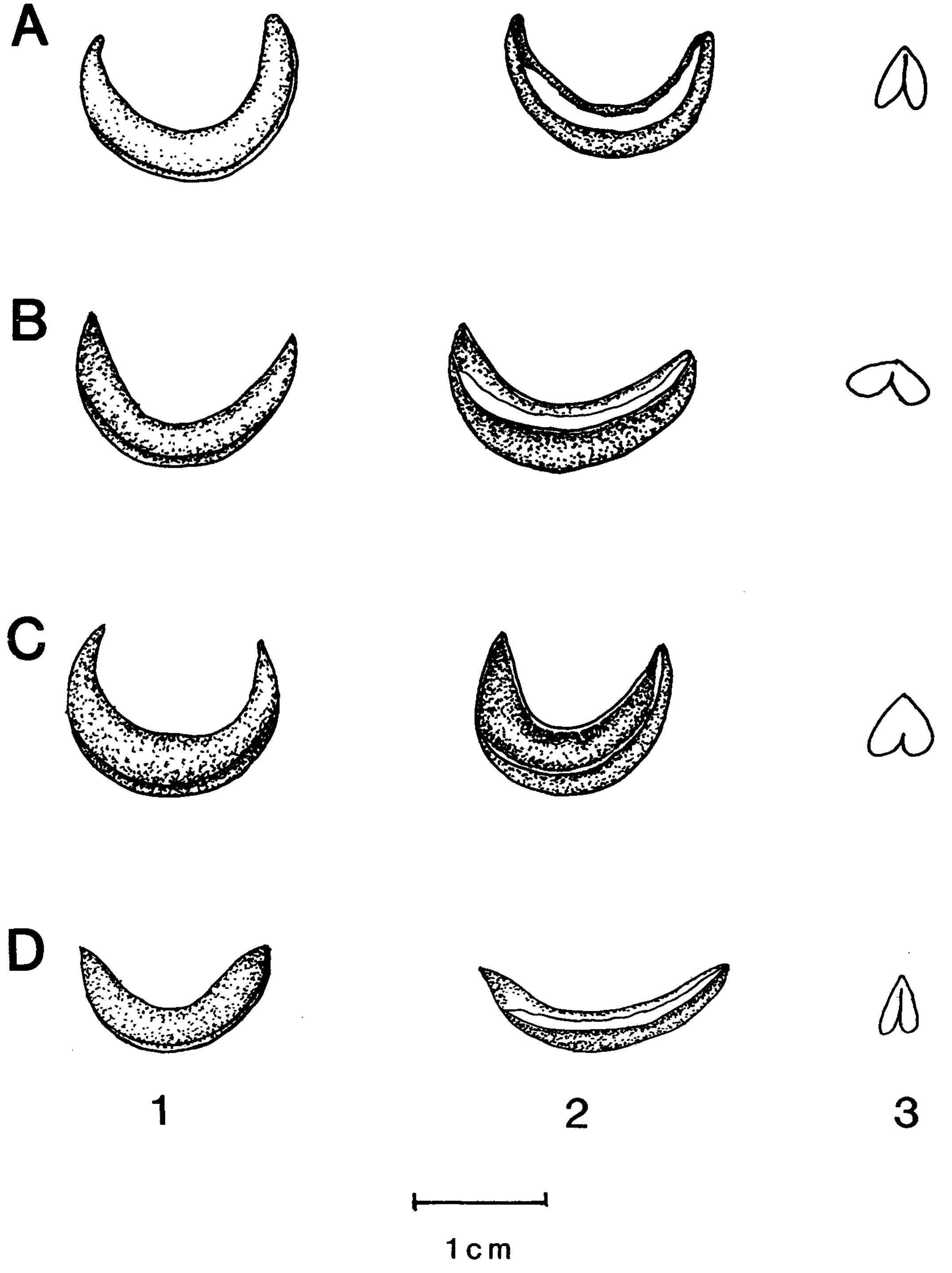


Figure 6. Pods of Astragalus diaphanus var. diaphanus. 1. Whole pod; 2. Longitudinal section; 3. Cross-section. A. Eight Mile Creek, Middle Fork (Wright 1694 OSC); B. Squaw Creek (Wright 1687 OSC); C. South of Clarno (Wright 1675 OSC); D. 10 miles east of The Dalles (Peck 13754 WILLU).

gynophore rarely present, 0.2-0.4 mm. Pods are illustrated in Figure 7.

<u>Astragalus</u> <u>sparsiflorus</u> var. <u>sparsiflorus</u>: (27 sheets) Short-lived perennial, branches slender and numerous, prostrate, 10-35 cm long; leaves 2-6 cm long, petiole to 3-25 mm, leaflets 9-13 (15), length 3-7 mm by 2-5 mm wide; stipule 1.5-3.5 mm; peduncles slender, slightly shorter than the leaves, pedicel 1-1.5 mm at anthesis, elongating to 1.5-3 mm in fruit, persistent; bract 1-1.5 mm; racemes 1-5 flowered, calyx campanulate, the tube 1.3-2 mm long by 1.5-2 mm wide, the teeth 1.2-2 mm long; flowers ascending, corolla white with pink veins in the banner and the keel pink or purple tipped, the banner 5-7 (7.5) mm, wings 4-5.5 (6.5) mm and the keel 3-4 mm, anthers 0.25-0.3 mm; pods ascending to slightly declined, 5-8 (10) mm by 2.5-4 mm wide, overall height 3-5 mm, septum width 0.1-0.3 mm when present, ovules 4-8, seeds 1.7-1.8 mm, pods generally sessile, but gynophore, when present, 0.5 mm. Pods are illustrated in Figure 8.

<u>Astragalus</u> <u>sparsiflorus</u> var. <u>majusculus</u>: (19 sheets) Annual or short-lived perennial, branches 5-15 (30) cm long, prostrate; leaves 4-6.5 (8.5) cm with petioles 1-2 (2.5) cm long; leaflets 13-15 (17), 8-13 mm by 2.5-5 mm; stipule (2) 3-4 mm; peduncles shorter than the leaves, racemes 3-8 flowered, pedicels 1-1.5 mm at anthesis, 2-3 (4) mm in

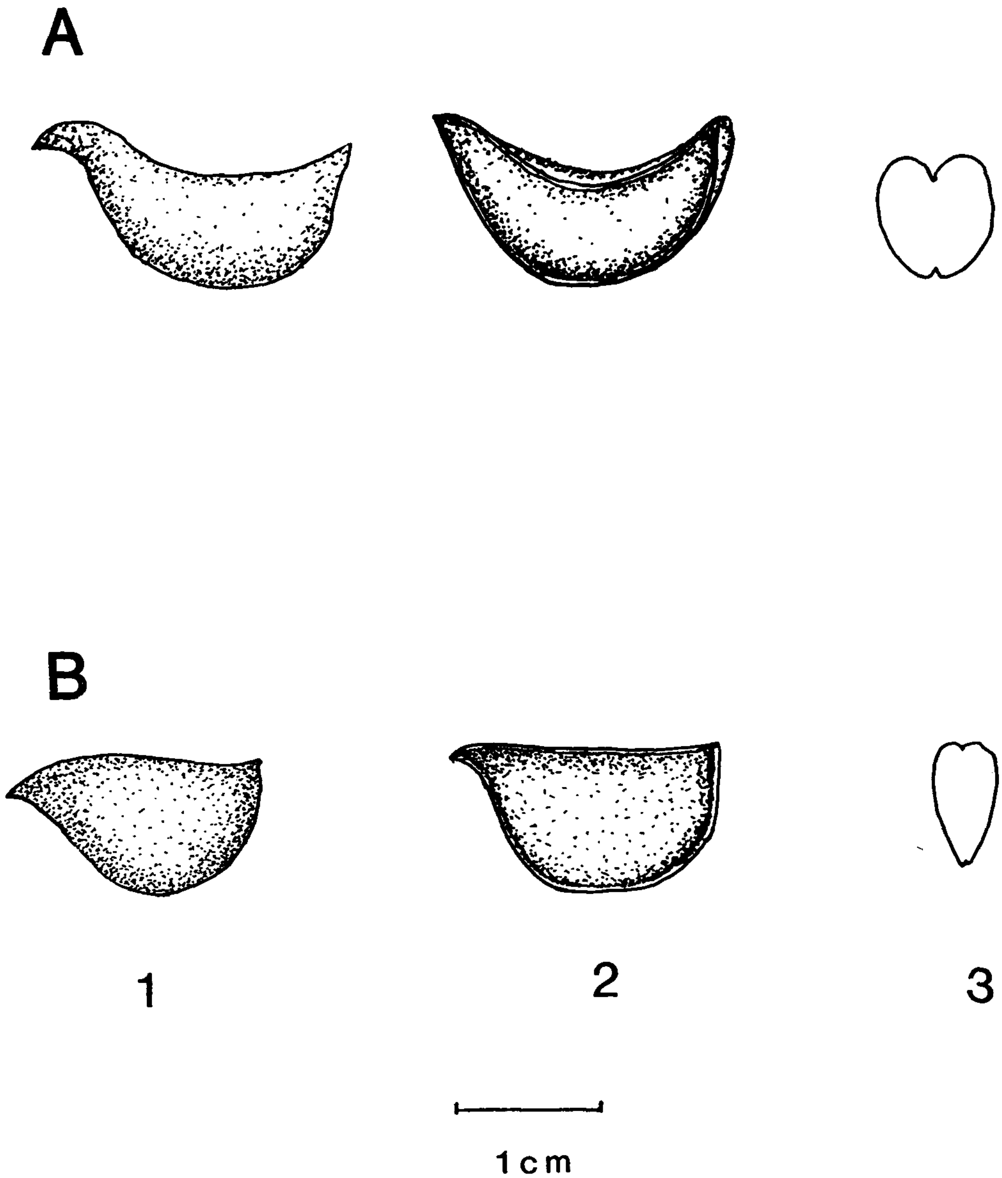


Figure 7. Pods of Astragalus diaphanus var. diurnus.
1. Whole pod; 2. Longitudinal section; 3. Cross-section.
A. Johnson Creek, typical form (Wright 1677 OSC);
B. Johnson Creek, flattened form.

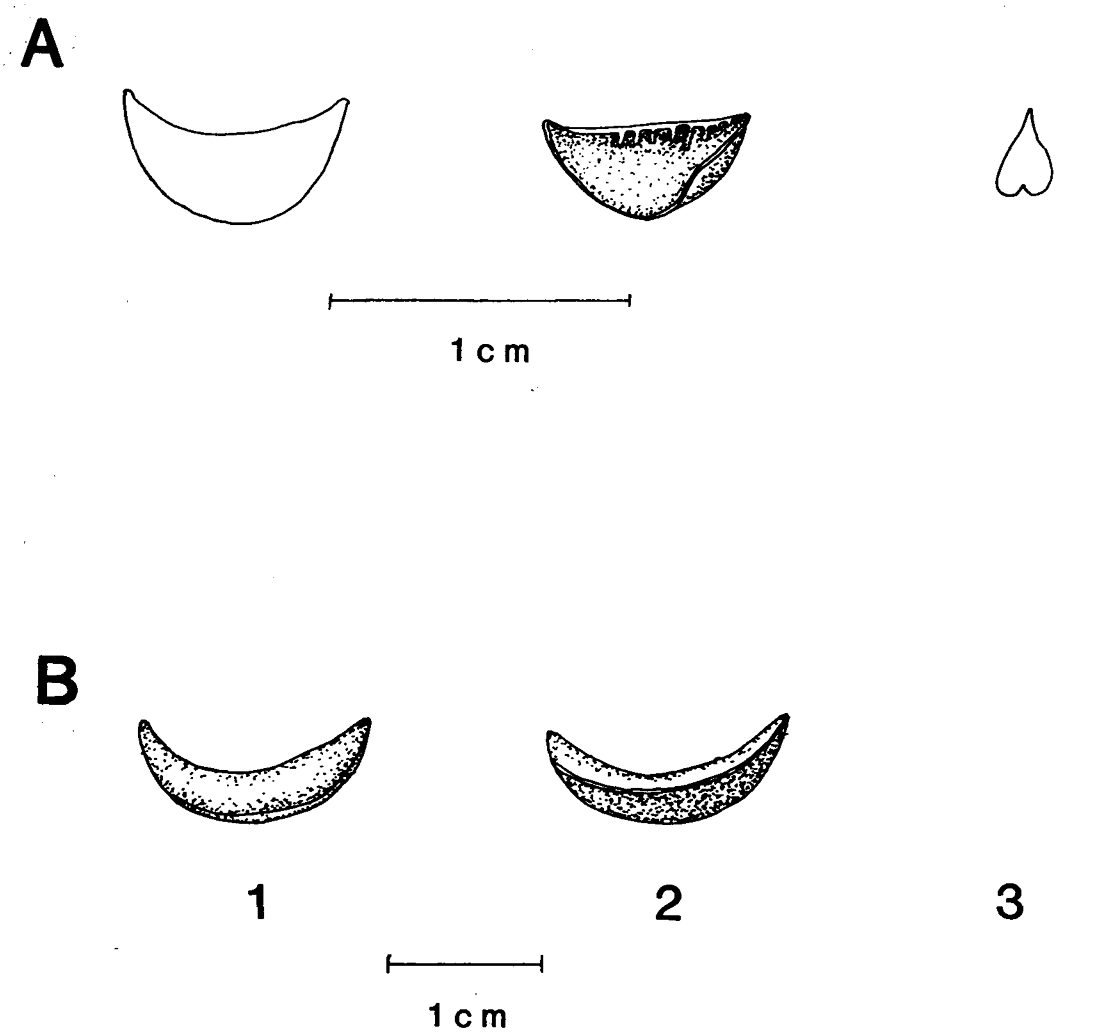


Figure 8. Pods of Astragalus sparsiflorus var. sparsiflorus and var. majusculus. 1. Whole pod; 2. longitudinal section; 3. cross-section. A. var. sparsiflorus (Ramaley 1378 COLO); B. var. majusculus (Weber, Wingate and Stevenson 16739 COLO).

fruit, persistent, bract 1.5-2 mm; calyx shallowly campanulate, the tube 1.7-2 (2.5) mm long by 1.5-2 mm wide with teeth 1-2 mm; banner white with pink or purple veins, 6-7 (8) mm, wings 5-6 (6.5) mm, keel purple tipped, 4-5 mm, anthers 0.2-0.3 mm, flowers ascending to spreading; pods ascending to slightly declined, 11-20 (25) mm by 3-4 (6) mm, with a total height of 4-9 mm, septum 0.2-0.5 (0.7) mm, ovules 10-14, seeds 2.1-2.5 (2.9) mm by 1.7-1.9 mm. Pods are illustrated in Figure 8.

Astragalus wetherillii: (29 sheets) Short-lived perennial, branches decumbent or ascending, up to 25 (35) cm long, leaves 4.5-7 (9) cm with 15-30 mm long petioles and 9-13 leaflets, leaflets 5-14 mm by (3) 4-8 mm, glabrous above, stipule 2-4 (5) mm; peduncles shorter than the leaves, racemes 3-8 flowered, pedicels 1-2 mm at anthesis, 2-2.5 mm in fruit, persistent, bract 1-2 mm; calyx campanulate, tube 2.5-3.5 mm long by 2-2.5 mm wide with teeth 1.5-3 mm; corolla white, banner 8.5-11 mm, wings 7-9 mm, keel 6-9 mm, anthers 0.4 mm; pods inflated, spreading to declined, elevated on a gynophore 1.5-2.5 mm, 15-22 mm long by 6-11 mm wide, funicular flange 1-1.2 (2) mm, septum when present 0.2-0.3 mm, ovules 8-12, seeds 2.6-3.1 mm by 1.5-2 mm.

Figures 6 and 7 illustrate pods of *A. diaphanus*. Shown in Figure 7 are two pod forms observed for var. *diurnus*, the common inflated form and a second form (only encountered on one plant) which is flattened on the sides rather than inflated, but otherwise looks very similiar to the common type. This appears to be an example of developmental plasticity within a population. The drawings of pods of var. diaphanus seen in Figure 6 illustrate the shapes found in various portions of the range. The pods from Squaw Creek are comparable to those called A. craigii, the morphology of which may possibly be the result of past hybridization between the two varieties. These pods have septa ranging in width from 0.5-1.2 mm. Pods of var. diurnus have a septum of 0.2-0.4 mm while typical var. diaphanus pods have a septum of 0.7-1.6 mm. The pods from Squaw Creek have a deeply intruded lower suture resulting in a nearly two-celled pod, but the pod is somewhat inflated in contrast to pods from populations farther down river. The pods from the remaining populations illustrated show the variability but also the overall similarity of forms within the species. I did not find there to be a gradation from one form to the next, as Barneby suggested. Of interest in this regard is the population from south of Clarno, whose pods essentially lack a septum. This population is the only one known which does not occur on Columbia River basalt. As far as can be determined, it is isolated from all other populations, although it is intermediate along the river between the populations near Service Creek and the historically known populations near the mouth of the John Day River.

CHROMOSOMES

Materials and Methods

Mitotic chromosome counts were made from root tips of recently germinated seeds. Fresh roots were treated in a saturated aqueous solution of paradichlorobenzene for two hours, rinsed with distilled water, fixed in 95% ethanol: glacial acetic acid (3:1) overnight, then rinsed in and transferred to 70% aqueous ethanol and stored in a freezer until analysed. Material was stained in Snow's acetocarmine stain at 45° C overnight. Slides were prepared using one drop each of 45% acetic acid and Hoyer's mounting medium, squashed, then examined under oil immersion using a Zeiss phase-contrast compound microscope.

Results

Counts were obtained for *A. diaphanus* var. *diaphanus* (*Wright 1694*), *A. diaphanus* var. *diurnus* (*Wright 1677*), and *A. sparsiflorus* var. *majusculus* (*Weber*, *Wingate*, and *Stevenson 16739* COLO). The count for both varieties of *A. diaphanus* is 2N=28. *Astragalus sparsiflorus* var. *majusculus* has a count of 2N=24.

Discussion

Old World species of Astragalus commonly have a base chromosome number of N=8. Chromosome numbers of New World species are either the same as Old World species or occur in an aneuploid series of N=11-15, with N=11 or 12 the most common (Barneby 1989). The 2N=28 count for A. diaphanus (also reported by Head 1957) is very unusual. This number has been reported previously in the New World for A. hypoleucus in Sect. Hypoleuci (Barneby 1964), A. sinaloae in Sect. Miselli and A. nothoxys in Sect. Leptocarpi (Spellenberg 1981; Goldblatt 1984). It has also been reported for two annual species in Portugal (Fernandes, Santos and Fatima 1975; Goldblatt 1981), a species in Spain (Pretel and Sanudo 1978; Goldblatt 1984) and one species in Russia (Bochantseva 1972; Goldblatt 1981). Variety diurnus and A. sparsiflorus had not previously been counted. Chromosome numbers for the the two remaining taxa in subsect. Sparsiflori are unknown. Within sect. Inflati, a count of 2N=24 has been reported for A. sabulonum (Spellenberg 1981). All other taxa in sect. Inflati for which counts have been published have 2N=22. The majority of Astragalus species have never had chromosome counts reported.

FLAVONOIDS

Materials and Methods

Dried plant material from two populations of *A. diaphanus* var. *diaphanus* (2 miles east of Service Creek, *Wright 1674* OSC, and Squaw Creek, *Wright 1687* OSC) and two populations of var. *diurnus* (Johnson Creek, *Wright 1677* OSC, and north of Jackass Creek, *Wright 1510* OSC) was used for flavonoid analysis. I followed the basic procedure of Wilkins and Bohm (1976). Flowers and leaves were analysed separately by two-dimensional thin-layer chromatography (TLC). Flower extracts were used to identify the flavonoid compounds.

Material was extracted in 80% aqueous methanol for five days. The extract was dried to a syrup using a flash evaporator, treated with celite, sodium chloride and 95° C distilled water, and filtered. The filtrate was mixed with n-butanol in a separatory funnel, and the aqueous solution discarded. The remaining butanol solution was taken to complete dryness; the flavonoids were resuspended in methanol and stored in vials. A preliminary separation was obtained by two-dimensional TLC using polyamid plates. The plates were first run in an "aqueous" solvent consisting of water/n-butanol/acetone/dioxane (210:45:35:20), dried and then turned 90 degrees and run in an "organic" solvent of benzene/ methanol/2-butanone/water (55:20:22:3). The plates were examined with long-wave ultraviolet light, sprayed with diphenylboric acid ethanolamine complex and reexamined with the UV light. A color map of the spot pattern was drawn for each sample.

Comparison of the two-dimensional TLC plates indicated a possible difference in the flavonoid diglycosides between the two varieties, so the two samples of each variety were pooled and run, respectively, through a Sephadex LH-20 gel filtration column. Separation into triglycoside, diglycoside and monoglycoside components was achieved by stepwise elution with 20% aqueous methanol, followed by 30%, 40%, 50%, 60% and 80% aqueous methanol. Bands were detected by long-wave ultraviolet light and collected in variable size fractions, then taken to complete dryness using a flash evaporator.

Fractions were again subjected to two-dimensional chromatography on polyamid, and visualised as before. Plates were viewed both before and after spraying using the UV light, and color spot maps were made.

To identify the monoglycosides, the fifth and sixth fractions of each sample were banded on polyamid plates and run in the "organic" solvent. The resulting bands were scraped from the plates, filtered using methanol and water, and brought to complete dryness using the flash evaporator. The compounds were confirmed to be monoglycosides by comparing them to known standards using polyamid TLC in the "organic" solvent. Identification was achieved by comparing the unknowns with standards using silica plates (Polygram Sil G) in a solvent of n-butyl acetate/acetic acid/water (75:20:5).

The diglycosides (fraction three of each sample) were purified in the same manner as previously described. Hydrolysis, to cleave the sugars, was done by placing small amounts of each sample band into two test tubes each (8 total), adding water and five drops of trifloroacetic acid to each tube, then placing the tubes into a boiling water bath. For partial hydrolysis a test tube of each pair was removed from the water bath after five minutes, placed in an ice water bath, and ethyl acetate and butanol added to each tube, resulting in a separation of the sugars and aglycones. The sugar-water mixtures were taken to complete dryness, rehydrated with two drops of methanol/water (1:1) and chromatographed on cellulose paper (Polygram Cel 300) in ethyl acetate/pyridine/water (10:3.2:2) twice, sprayed with p anisidine phthalate spray reagent and baked at 110°C for five minutes. Unhydrolyzed flavonoid was completely dried, resuspended in methanol and chromatographed on silica plates against monoglycoside standards.

Full hydrolysis of the remaining four samples was done by boiling for one hour, with an additional five drops of trifloroacetic acid added to each tube after one-half hour. Sugars were separated from the aglycones and tested against standards as previously described. There was an insufficient amount of the aglycones to test.

Structural Determination

Determination of the aglycone identities and points of sugar attachment was done using UV spectroscopy with spectral reagents (Mabry et al. 1970). From each flavonoid analysed a small concentrated amount was added to spectral methanol in a quartz cuvette. A spectral scan between 420 nm and 240 nm was obtained using a Beckman model 25 spectrophotometer. After the initial scan the solution was saturated with anhydrous sodium acetate, scanned, then neutralized with powdered boric acid and scanned for a third time.

Results

The two-dimensional TLC revealed 8 compounds, 7 in large enough quantities to analyse. Spot maps of the four samples are in Figures 9 and 10. There were also some very faint spots seen which were mapped but not identified.

Spot #1 was yellow under UV light prior to spraying

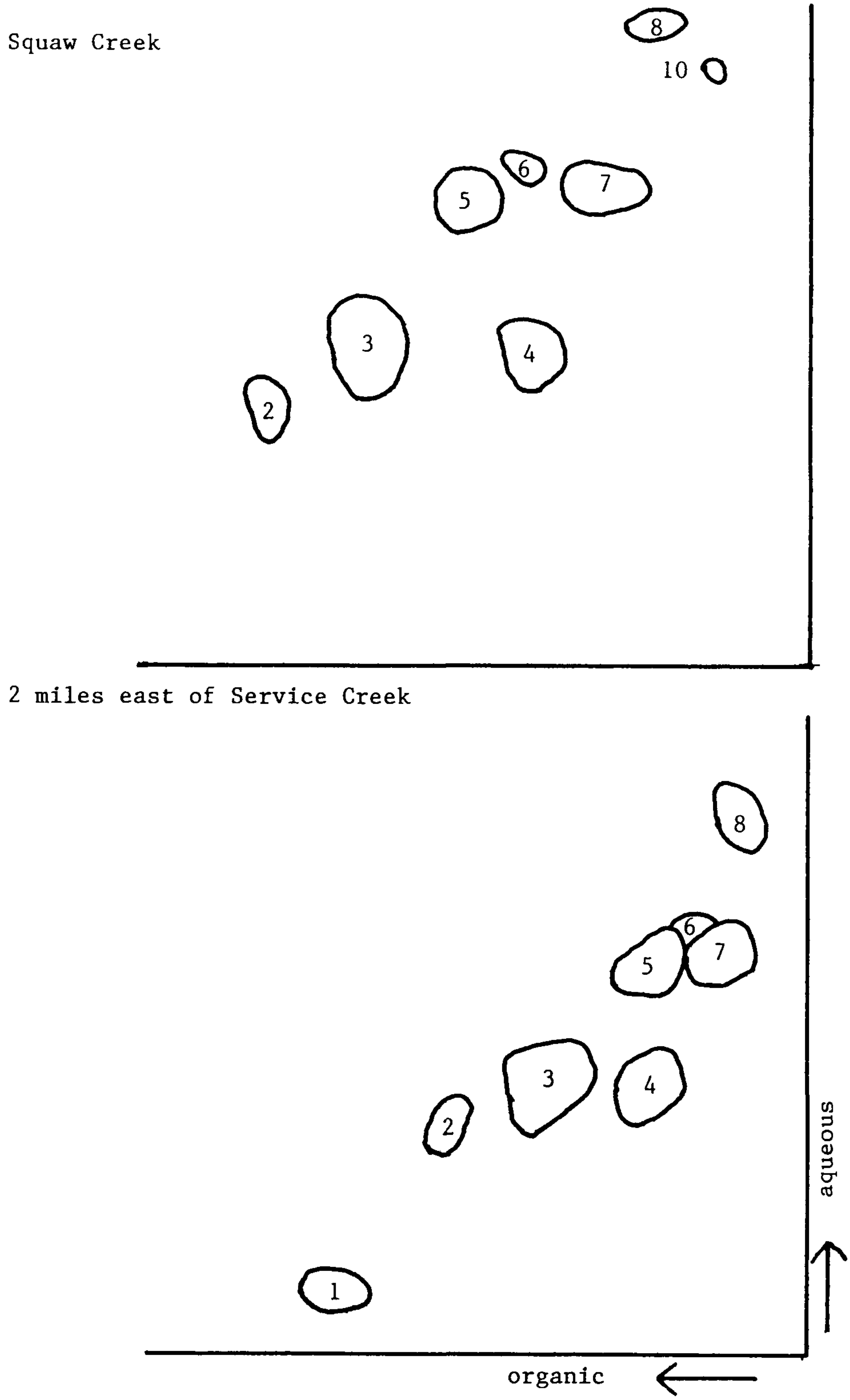


Figure 9. Two-dimensional thin-layer chromatography spot maps of Astragalus diaphanus var. diaphanus.

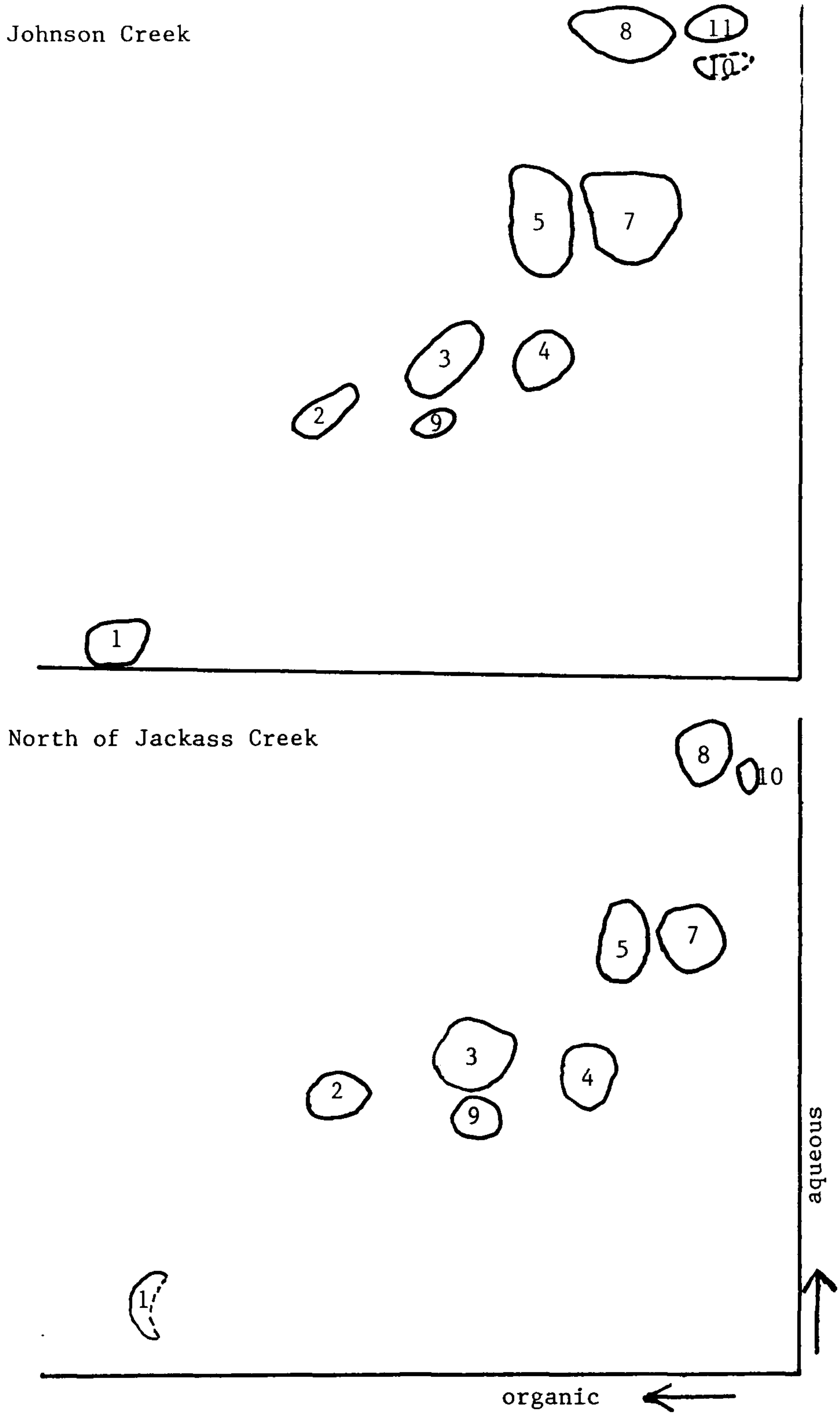


Figure 10. Two-dimensional thin-layer chromatography spot maps of *Astragalus diaphanus* var. *diurnus*.

with diphenylboric acid ethanolamine complex. After spraying it was blue-green, indicating it is a flavonol. All other spots were purple under UV light, and yellow or green under UV light after spraying. The colors indicated that quercetin (orange-yellow), syringetin, isorhamnetin and/or kaempferol (green) might be present (Wilkins and Bohm 1976). The relative positions of the spots indicated the presence of three monoglycosides, two to three diglycosides and one triglycoside (J.M. Miller pers. comm.). The two plates of var. diaphanus each had a third diglycoside spot which was not present on the plates of var. diurnus. The Rf values of the spots and their colors are listed in Table 7.

TABLE 7: Two-dimensional thin-layer chromatography Rf values and spot colors for Astragalus diaphanus.

SPOT No.	COLOR	COMPOUND	Rf VALUE X 100 ORGANIC:AQUEOUS BY SITE 2ESC	SQCK	JACK	JOCK
1	Y:BG	Flavonol	53:7		69:11	63:9
2	P:YG	Monoglycoside	38:26	58:25	48:25	42:27
3	P:YG	Monoglycoside	27:30	46:31	35:30	31:32
4	P:Y	Monoglycoside	16:30	29:30	23:28	22:32
5	P:YG	Diglycoside	16:44	35:44	19:40	23:47
6	P:YG	Diglycoside	13:41	29:48		
7	P:Y	Diglycoside	8:45	20:46	12:41	14:47
8	P:YG	Triglycoside	6:60	14:62	11:59	15:66
9	?:YO	Unknown			34:24	32:26
10	?:YO	Unknown		8:58	6:57	7:63
11	?:YO	Unknown				7:67

Spot Number is taken from TLC spot maps. Colors: P = purple, Y = yellow, YG = yellow-green, BG = blue-green, YO = yellow-orange. Organic solvent: benzene/methanol/2-butanone/water (55:20:22:3). Aqueous solvent: water/n-butanol/acetone/dioxane (210:45:35:20). 2ESC = 2 miles east of Service Creek; SQCK = Squaw Creek; JACK = north of Jackass Creek; JOCK = Johnson Creek.

Five monoglycosides were isolated and identified. One of these compounds, Isorhamnetin-3-O-xyloside, was isolated only from var. diaphanus. I suspect that it also occurs in var. diurnus, but that there was an insufficient amount present to be analysed. There was no difference in the spot maps in the monoglycosides.

Two diglycosides were partially identified, but it was not possible to identify all of the sugars. During hydrolysis the two sugars were cleaved together, so I was unable to get a transient intermediate monoglycoside or separate sugars. The sugar test was not conclusive: glucose is present and galactose is probably also present, but unconfirmed. Other sugars which may be present are unknown. Further analysis is needed to determine if the diglycoside difference indicated by the spot maps does exist between the two varieties.

The triglycoside and the flavonol were not identified. Table 8 lists the compounds isolated and in which variety they occurred.

Peak values of the spectral scan are presented in Table 9. Appendix II contains reproductions of the scans. There was variation in the peaks between the different samples which were presumed to be the same compounds. Mabry et al. (1970) state that the λ max spectral values are not readily

TABLE 8: Flavonoids isolated from *Astragalus diaphanus* var. *diaphanus* and var. *diurnus*.

COMPOUND ISOLATED	VARIETY diaphanus	VARIETY diurnus
Unknown flavonol	X	X
Isorhamnetin-3-*O*-xyloside	X	
Kaempherol-3-*O*-galactoside	X	X
Kaempherol-3-*O*-glucoside	X	X
Quercetin-3-*O*-galactoside	X	X
Quercetin-3-*O*-glucoside	X	X
Kaempherol-3-*O*-diglycoside	X	X
Quercetin-3-*O*-diglycoside	X	X
Unknown triglycoside	X	X

TABLE 9: Spectral values obtained for flavonoids isolated from *Astragalus diaphanus*.

FRACTION BAND*	PUTATIVE COMPOUND	BAND I: BAND II** MeOH	NaOAc	$NaOAc/H_3BO_3$
SFJDR-3-slow	Quer. digly.	354sh:254	386sh:268	368sh:260
JDR-3-slow		357sh:259	382sh:269	378sh:261
SFJDR-3-fast	Kaem. digly.	342:268	369sh:273	352sh:268
JDR-3-fast		351sh:267	374sh:273	352sh:267
SFJDR-5-slow	Quer. mono.	none	none	none
JDR-5-slow		:256sh	383sh:271sh	360sh:262
SFJDR-5-med.	Kaem. mono.	347:267	373sh:273	351:267
JDR-5-med.		351:267	377sh:274	352:266
JDR-6	Iso. mono	:269sh	:273sh	:269sh

*Fraction band identifies variety (SFJDR = var. *diurnus*, JDR = var. *diaphanus*; number refers to fraction from gel filtration column; and speed refers to band separation from polyamid plates.
**Band I is spectral length between 420 and 340nm; Band II is spectral length between 340 and 240nm. Sh refers to a shoulder.

reproducible when using NaOAc and NaOAc + H_3BO_3. They further state that the shapes of the spectral curves are more reliable guides for identification purposes. Consultation with a person experienced in analyzing flavonoid spectral charts is needed to interpret the data obtained. Additional flavonoid analysis which would include the Colorado species and other species from the closely related subsect. Aridi might be helpful in clarifying relationships among species.

Discussion

All of the flavonoid compounds that were isolated and identified are common among angiosperms (Harborne et al. 1975; Mabry et al. 1970). As shown by Table 8, five of the six identified mono- and diglycosides are identical in the two varieties of A. diaphanus. Isorhamnetin-3-O-xyloside, although found only in var. diaphanus, may be expected in var. diurnus as well, if a larger amount of test sample could be extracted. The unknown flavonol and unknown triglycoside were also present in both varieties. This marked similarity in flavonoid profiles of the two taxa under study supports their being assigned as varieties of a single species. If a significant difference in flavonoids had been discovered between them, this might have led to higher taxonomic ranking of the two types, which as earlier noted are conspicuously different in pod morphology.

There has not been any large-scale systematic work done with flavonoid analysis in North American *Astragalus* species. In Russia, extensive chemical studies of flavonoids isolated from *Astragalus* have been performed, (Chemical Abstracts 1981-1985), but the literature does not indicate that the data were applied to systematic revisions of the genus.

PHYLOGENY

Primitive and Advanced Characteristics

Barneby (1964) discusses primitive and advanced characteristics of *Astragalus* and *Oxytropis* (a closely related genus segregated from *Astragalus*) as a basis for the phylogenetic treatment of *Astragalus*. His summary of the characters follows:

1. Herbaceous perennials gave rise to annual and shrubby types.

2. Connate stipules, at least in recent time, precede free ones.

3. A loosely racemose inflorescense is primitive to densely racemose, spicate, subumbellate, or capitate ones.

4. A nodding flower and pendulose pod precede an ascending or erect flower or fruit.

5. A campanulate calyx and relatively short-clawed petals precede a cylindric calyx and long-clawed petals.

6. An emmenoloboid pod precedes a piptoloboid one, and a deciduous pedicel precedes one which becomes thickened and persists with the fruit.

7. A papery pod precedes a membranous, leathery, fleshy or pithy one.

8. A trigonous mode of compression gives rise, either with or without a septum, to laterally flattened, dorsiventrally flattened, or terete (or more elaborately modified) types.

9. Although the septum is assumed to be an acquired character, no inference can be drawn from its presence or absence in contemporary North American species.

10. Each of these sequences has occurred

independently in various lines of inheritance; each is subject to reversal.

11. A chromosome complement in multiples of 8, the number commonest among the Galegeae, gave rise, possibly by means of reduction subsequent to tetraploidy, to the highest numbers prevalent in America; but no identifiable external morphological change accompanied this cytological development.

Table 10 lists the above characters (1-8) and rates the taxa of subsect. Sparsiflori taxa for primitive and advanced characters.

TABLE 10: Primitive and advanced characters of subsect. Sparsiflori

PRIMITIVE/ADVANCED CHARACTER	TAXA* ASDI	ASDI2	ASSPM	ASSPS	ASWH
Perennial/annual	A	A	P	P	P
Connate stipules/ Free stipules	A	A	A	A	A
Loosely racemose/ Otherwise	P	P	P	P	P
Nodding flower/ Erect or Ascending	A	A	A	A	A
Nodding pod/ Erect or ascending	P	P	A	A	P
Campanulate Calyx/ Cylindric calyx	P	P	P	P	P
Short-clawed petals/ Long-clawed petals	A	A	A	A	A
Emmenoloboid pod/ Piptoloboid pod	A	A	A	A	A
Deciduous pedicel/ Thickened, persistent	A	A	A	A	A
Papery pod/ Other types	A	A	P	P	P
Trigonous compression/ Pod otherwise	A	A	A	A	A

A=Advanced character, P=Primitive character.
*ASDI = _Astragalus_ _diaphanus_ var. _diaphanus_, ASDI2 = _A_. _diaphanus_ var. _diurnus_, ASSPM = _A_. _sparsiflorus_ var. _majusculus_, ASSPS = _A_. _sparsiflorus_ var. _sparsiflorus_, ASWH = _A_. _wetherillii_.

Barneby stresses that in *Astragalus* the reproductive organs, in particular the fruiting body, are quite plastic and readily undergo genetic and evolutionary change, even between closely related taxa. This is in contrast with most flowering plants, where the reproductive organs are the most conservative evolutionarily and the most reliable for determining affinities both within a genus and between genera and families. This variability of pod shape is apparent in *Astragalus diaphanus*, perhaps providing the best example within the genus of how readily the pod can evolve different shapes. *Astragalus sparsiflorus* also has distinct pod forms between the two varieties, but they are more recognizable as being related. Consequently, other characters are utilized by Barneby in determining affinities, both within this subsection and throughout the genus.

Emmenoloboid pods are persistent on the raceme, in contrast to piptoloboid pods which are deciduous from the raceme. Emmenoloboid pods are considered the primitive form. However, deciduous pedicels are considered primitive to those which have become thickened and persist with the pod. Barneby considers the septum to be an advanced character, but does not consider its presence or absence to be helpful in determining phylogenies. Many of the traits are considered to be readily reversible.

Relationships of the Species

Barneby (1964) discussed at length his placment of the three species in a separate subsection Sparsiflori, rather than including them in the closely related subsection Aridi. *Astragalus wetherillii* and *A. diaphanus* var. *diurnus* are very similiar to members of subsection Aridi with their simple, inflated pods. However, with the inclusion of the more specialized pod forms of var. *diaphanus* and *A. sparsiflorus*, Barneby felt the subsection was a valid entity. My studies do not provide either supporting or conflicting data to address the affinities of the three taxa, but I believe their possible relationship to subsect. Aridi is still an open question.

I do agree with Barneby in considering *A. diaphanus* var. *diurnus* to be more primitive than var. *diaphanus*. The pods of var. *diaphanus* are more complex, with a wide septum, dorsal groove, and triquetrous compression, in contrast to the simple, inflated pods of var. *diurnus*. Likewise, Barneby considered *A. sparsiflorus* var. *majusculus* to be the simpler and more primitive variety of that species. Overall, var. *sparsiflorus* is a more delicate plant, with most of its structures of a smaller size than in var. *majusculus*. It, too, has a broader range in comparison with its related variety.

LIFE HISTORY OF ASTRAGALUS DIAPHANUS

Astragalus diaphanus functions as both an annual and a biennial. When I initiated this study in 1983, there were several populations which had robust biennials flowering and fruiting at the time seedlings were present. I was uncertain about when the biennials had germinated--were they actually winter annuals or true biennials? I wondered if the seedlings were progeny of the plants present, or if they had germinated from a seed bank. I also wondered how many plants were annuals and how many became biennials, and what the relative reproductive success was of the two strategies.

Methods

Two sites of var. *diaphanus* and one of var. *diurnus* were visited regularly for 14 months from April 1984 through May 1985. In May 1984 I began to track individual plants, recording date first observed, growth, flowering, fruiting and fate. All biennial plants found at each site were tracked, plus a sampling of seedlings. By September 1984 most of the individuals being tracked had died. However, there were other plants alive at each site, so a new set of individuals was chosen and tracked. The same data were kept on these individuals. Information about the study sites and number of individuals tracked at each locality is in Table 11. In addition, phenological and reproductive data were collected each time any other population was visited.

TABLE 11: Site information and number of individuals tracked.

SITE	FIRST YEAR Biennials	FIRST YEAR Annuals	SECOND YEAR Biennials
2 mi E Service Creek	2	37	12
Homestead	4	68	16
Johnson Creek	1	21	15 (+30)*

*Plants counted only, no reproductive data collected.

Other aspects of the field studies were to observe pollinators and other insect visitors of the *Astragalus*, and to make general observations concerning the plants. Greenhouse studies were conducted in an attempt to hybridize the two varieties; as part of this work information was collected concerning seed germination.

First Season Phenology

Seedlings of *A. diaphanus* were first seen in late March, with most seedlings apparent by early May. Late-season rains may stimulate additional germination. Anthesis began in mid-May, with most plants flowering by late May. Pods first appeared in late May and were common by early June. Most plants (86%) were dead by mid-July, and less than 6% were still alive in September. Figure 11 presents phenological data about the first season.

Figure 11. Annual phenology of *Astragalus diaphanus*.
= vegetative; = flowering;
= fruiting; = dead.

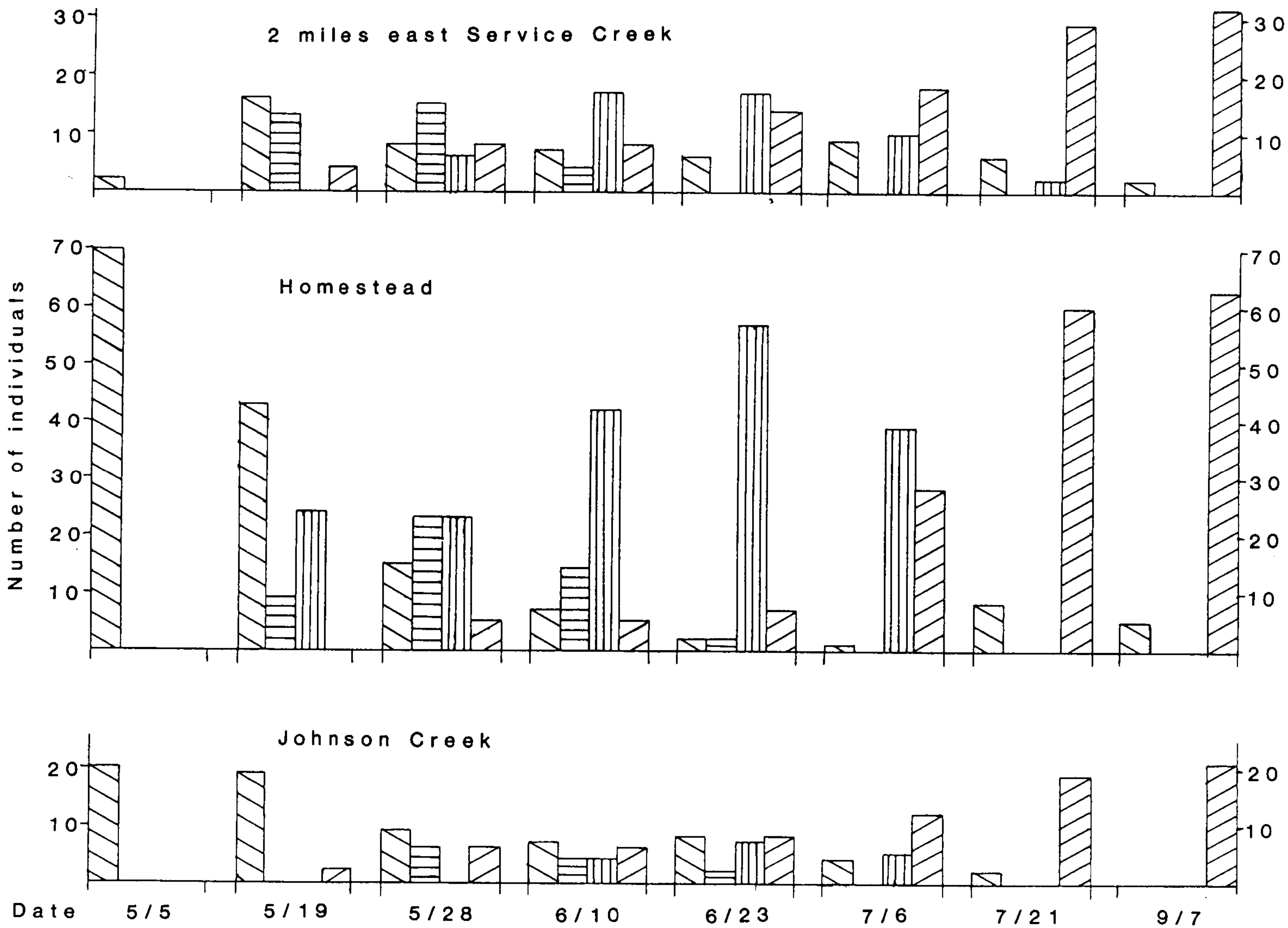

2 miles east Service Creek
Homestead
Johnson Creek
Number of individuals
30
20
10
70
60
50
40
30
20
10
20
10
Date
5/5
5/19
5/28
6/10
6/23
7/6
7/21
9/7

Figure 11

Biennial Phenology

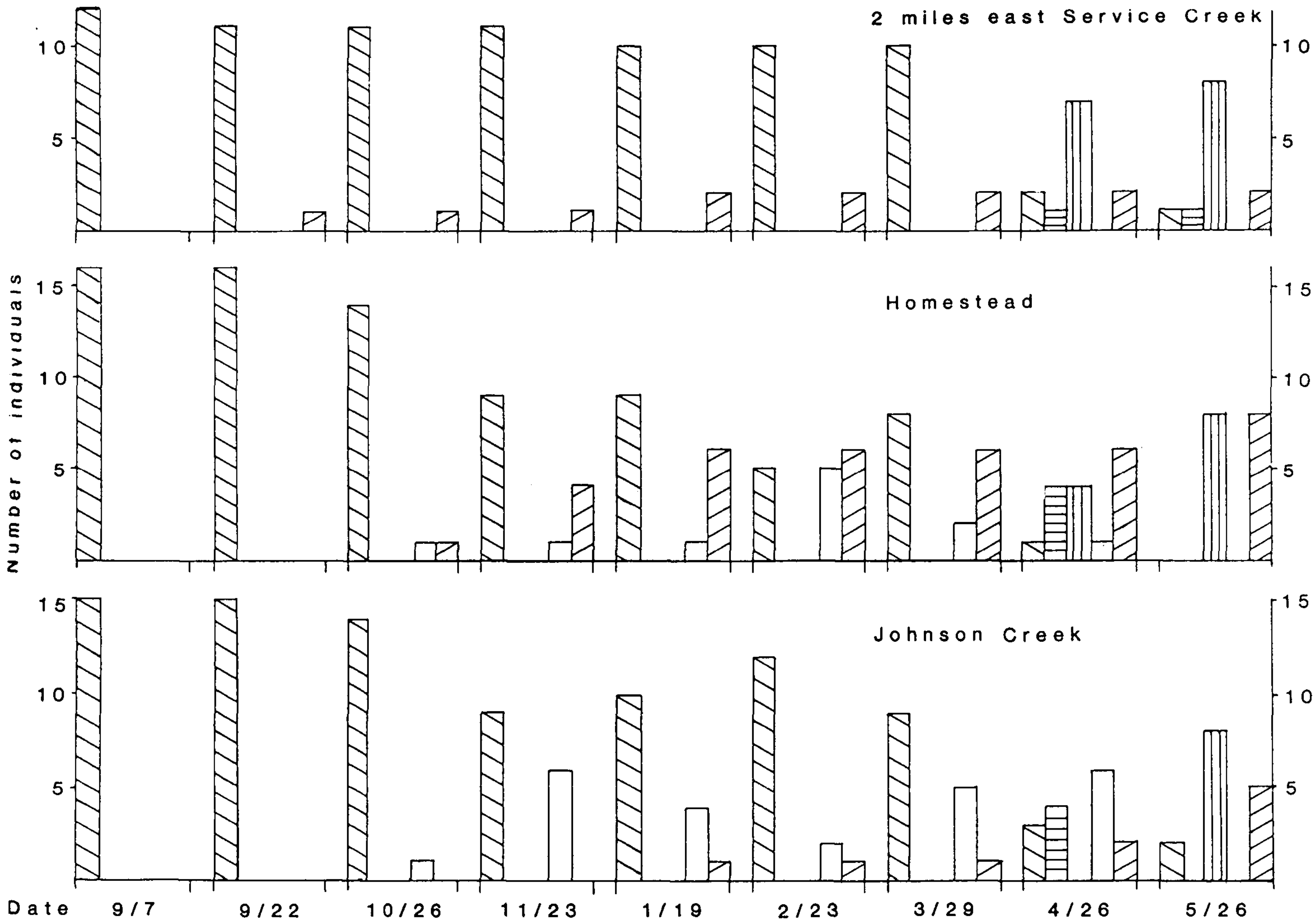
Plants surviving the summer continued to grow slowly through the fall and winter months. A 21.9% (N=73) mortality rate occurred between September and late March. The highest rate was at the Homestead site with 37.5% (N=16) mortality, while mortality at the site 2 miles east of Service Creek (2ESC) was low at 16.7% (N=12) and mortality at the Johnson Creek site had a 17.8% (N=45) loss. In March the growth rate accelerated, with flowering and fruiting beginning in April and continuing through May. In June the plants began to senesce, and all were dead in July. Figure 12 presents survival and phenological data for the biennials.

Reproductive Success

Annuals at all three sites had an average reproductive rate of 71.4% (N=126) (plants producing pods). Of these, the average number of pods produced per plant was 3.6. The number of pods per plant ranged from one to nine. 2ESC had a 62% (N=37) average reproductive rate with 3.1 pods per plant and a range of 1-6 pods. Homestead had an 85.3% (N=68) average reproductive rate with 3.92 pods per plant, ranging from one to nine. Johnson Creek had a 43% (n=21) reproductive rate with 4.1 pods per plant and a range of 1-9.

Biennials generally had better reproductive success

Figure 12. Biennial phenology of Astragalus diaphanus.
= vegetative; = flowering; = grazed;
= fruiting; = dead.



2 miles east Service Creek
Homestead
Johnson Creek
Number of individuals
10
5
15
Date
9/7
9/22
10/26
11/23
1/19
2/23
3/29
4/26
5/26

Figure 12

than annuals if they survived to the second spring. All of the biennials tracked in the first spring of the study produced pods, averaging 42.2 pods per plant with a range of 1-109 pods per plant. Of the biennials followed from September through May, 55.8% (N=43) produced fruits, with an average of 22.5 pods per plant. At 2ESC, the reproductive rate was 66.7% (N=12), with 26.4 pods per plant and a range of 6-58. At Homestead there was a reproductive rate of 50% (N=16), with 12.1 pods per plant and a range of 3-25. At Johnson Creek the reproductive rate was 53.3% (N=15), with 30.7 pods per plant and a range of 1-60.

Plants observed at other locations showed the same range in the number of pods produced. Several biennials have been observed with over 100 pods; the highest number counted was 190.

Herbivory, Insects, and Disease

Herbivory during fall and winter was an unexpected observation. I assume that deer were the cause of the substantial damage and loss to plants. Overall, 62.8% (N=43) of the plants tracked were damaged to some extent by herbivory. The range of values was from 25% at 2ESC to 62.5% at Homestead and 93.3% at Johnson Creek. In some instances only minor damage was sustained; at other times the plant was left with only branch stubs or was completely gone. Some of the plants were able to recover and reproduce, but there was definite mortality associated with the herbivory as well. On one occasion a fruiting biennial plant was observed which a mouse or other small mammal had visited and had eaten many of the seeds. Pod remains had been chewed open and the seeds were gone.

Other forms of predation were observed. Spittle bugs, Aphrophora sp., feed on the stem at ground level on the second-year plants. A planthopper and several leafhopper nymphs and adults were collected from plants in May and June. Some of the leafhoppers and the planthopper were probably feeding on nearby grass. Leafhoppers feed by piercing the leaves and sucking juices. Larvae of Queen Alexandra sulfur butterflies, Colias alexandra, were collected from biennials at the end of March and were hatched in the greenhouse. These large green caterpillars have been observed on several occasions. Unidentified black aphids and attendant ants are common on biennial plants in June and July. In April and May extensive webbing and herbivory has been observed; however, the insect responsible is unknown. Insect predation of seeds was observed once; 16 pods out of 35 were affected.

An Acmon blue butterfly, Plebejus acmon, was collected from Astragalus at the Homestead site in late May. Its interactions with the plants is unknown; however, blue butterflies are often seen to be associated with legumes. No insects were observed pollinating flowers. A list of identified insects found in association with *A. diaphanus* is in Table 12.

TABLE 12: Insects found with *Astragalus diaphanus*.*

ORDER AND FAMILY	GENUS (or subfamily)	COMMON NAME
Hemiptera:		
Coreidae	*Cariomeris* sp. (near *occidentalis*)	leaf-footed bug
Dictyophaeridae	+*Scolops* sp.	planthopper nymph
Lygaeidae	*Geocoris* sp.	seed bug (predator)
Homoptera:		
Cercopidae	*Aphrophora* sp.	spittle bug (leafhopper)
Cicadellidae	*Aceratagallia* sp.	leafhopper nymph & adult
	+Deltocephalinae	leafhopper
	+*Xerophloea* sp.	leafhopper nymph
Lepidoptera		
Pieridae	*Colias alexandra*	Queen Alexandra sulfur
Lycaenidae	*Plebejus acmon* (*Icaricia*)	Acmon blue

*Nomenclature follows Borror, Triplehorn and Johnson (1989).
+Insects which are probably grass-feeders.

A rust, *Uromyces punctatus*, was reported to occur on *A. diaphanus* by Shaw (1973). Rust is common on biennials, becoming prominant late in the season with many lesions present on leaves and stems. Staff members of the OSU Plant Clinic were unable to identify the rust definitively, but thought it was probably the same one which was previously reported.

Seed Germination and Greenhouse Studies

Seeds from six populations were placed on white filter paper in petri dishes, watered, and kept at room temperature. The seeds had been collected the prior field season and stored at room temperature for approximately eight to nine months. Populations represented were from Johnson Creek (20 seeds), Squaw Creek (25 seeds), Homestead (11 seeds), Eight Mile Creek (25 seeds), 1.5 miles east of Three Mile School (20 seeds), and 4.5 miles east of Hwy 395 (41 seeds). In addition, another 18 seeds from a mixed collection were treated prior to soaking. Seed coats were nicked on ten seeds and seed coats were filed on eight. Unfortunately, I had problems with mold and many seeds rotted. In late May and June seeds from populations at Homestead (12 seeds) and 2 miles east of Service Creek (81 seeds) were collected and placed in petri dishes as before.

Seeds exhibited a variety of germination responses. All those which had their seed coats scarified were swollen within one day and began to germinate in two days. All of these seeds germinated within five weeks. Of seed left untreated, the percentage which became swollen within a week ranged from 8% of the seed from Eight Mile Creek and Squaw Creek to 45% of the seed from Johnson Creek. After seven months, 64% of the seed from Eight Mile Creek was still hard and only 12% of the seed had germinated. In contrast, 10% of the seed from 4.5 miles east of Hwy 395 remained hard after seven months and 44% had germinated. Table 13 gives the percentages of seeds swollen within the first week, germinated within seven months, and remaining hard after seven months.

TABLE 13: Germination rates of untreated seeds from selected sites of <u>Astragalus</u> <u>diaphanus</u>.

SITE	# SEEDS	%SWOLLEN 7 DAYS	%GERMINATED 7 MONTHS	%HARD AT 7 MONTHS
Johnson Creek	20	45	40	30
Squaw Creek	25	8	52	12
Homestead	11	18	36	45
8 Mile Creek	25	8	12	64
E 3 Mile School	20	20	20	60
E Hwy 395	41	39	44	10

* percentages do not total 100% due to seed mortality.

Seeds which were collected and soaked immediately did not necessarily show an after-ripening requirement. 52 of the seeds from 2ESC were wet while still in the field and became swollen immediately. Four of these seeds germinated within a month, and 73% germinated within four months. The remaining 29 seeds from 2ESC had a 34% germination rate within four months, and 58% of the seeds from Homestead had germinated in the same time. Fifty-nine percent of the 2ESC seeds remained hard after four months.

Seedlings were planted in a mixture of peat, sand, vermiculite and soil from Johnson Creek and kept in the greenhouse. There was a high mortality rate due to fungal infections and other unknown problems. Plants did not begin to flower until late October. In an attempt to cross-pollinate populations and varieties, pollen was transferred between flowers. However, I found that the flowers are self-compatible, and that it is not possible to transfer pollen without also self-pollinating the flowers. I attempted to emasculate the anthers prior to anthesis without success. I did show that it is necessary for the flowers to be "triggered" by insect visitors in order to be pollinated, and this was also demonstrated in the field. At the Homestead site I bagged flowering branches of biennial plants to exclude insects. There was no fruit production on the bagged branches but there was prolific production on the remaining unbagged branches.

I looked at reproductive success by counting the number of seeds produced per pod. Numbers of seeds per pod ranged from 0 to 13. Average number of seeds per pod were: Johnson Creek--4.7, Eight Mile Creek--6.0, 1.5 miles east of Three Mile School--4.9, 4.5 miles east of Hwy 395--4.1, and 2 miles east of Service Creek--6.8 seeds per pod.

DISCUSSION AND CONCLUSIONS

The relative rarity of Astragalus diaphanus contributed to the historic confusion over the taxonomic status of its two varieties. Although portions of its range received attention by collectors in the past, much of the area had never been explored by botanists. Variety diurnus had only been collected once in nearly 100 years. Consequently, there was not enough material historically available to reach a sound taxonomic judgement. There is a better understanding today of the full geographic range encompassed by the species, but that range has recently diminished as a result of habitat loss along the Columbia River. Perhaps seed is not dispersed downriver as readily as it had historically, because roads situated between the upland habitat of the species and the rivers pose a barrier to natural dipersal, and also because of the excessive use of the rivers for irrigation purposes (portions of the John Day River are pumped nearly dry at times).

Some of the morphological measurements I made of the five taxa differ substantially from those of Barneby (1964). With regard to dimensions of the corolla, the differences can be explained by the fact that I did not rehydrate the material as Barneby did. Otherwise, it may simply be that I worked with a greater volume of material than was available to him. Certainly with respect to A. diaphanus this was the case. I think it is interesting that var. diurnus constitutes a more narrowly defined (i.e. less variable) taxon overall than var. diaphanus, although its measurements all fall within the broader size ranges encompassed by the latter variety. It may be that with further collecting, var. diurnus will prove to be as diverse as var. diaphanus. Variety diaphanus exhibits interesting differences in pod morphology both within and between populations. However, these differences do not appear to be correlated with geographic distribution.

Although the flavonoid results were inconclusive, they do reflect the morphological similarity of the two varieties (exclusive of their pods) and they support treating the taxa as one species rather than two. The suspected occurrence of an additional compound in var. diaphanus favors the idea that there are two varieties within the species. The identical, and unusual, chromosome counts lend further weight to considering the taxa as varieties of a single species.

Barneby's placement of the three species into subsect. Sparsiflori does not seem to me to be an altogether natural grouping. However, I do not have evidence to contradict his taxonomy, nor do I have an alternative suggestion. Further study is needed to clarify the relationships of the three species.

Lowered reproductive rate in A. diaphanus appears to be a potential problem, possibly contributing to its rarity. There is a substantial loss when seeds germinate and the plants die without reproducing. It appears that the species may not yet have evolved a successful annual strategy; however, its environment is not conducive to a biennial strategy. Many associated perennials (Allium, Lewisia, Lomatium) are dormant in the summer months and are green from fall to spring. The moderate soil temperatures recorded and snow-free conditions observed through the winter indicate that such plants may be able to grow during the coldest months. Upon germinating, Astragalus plants appear to put a greater effort into developing their root system than into flowering and fruiting. This strategy can be used successfully by winter annuals (Bromus tectorum is a good example), but I am not aware of other spring annuals with a similiar strategy. In years of adequate precipitation, these plants are then able to survive the extreme heat and drought conditions of the summer months. However, only a very small percentage of plants survive to a second season and then are able to produce the tremendous numbers of pods I occasionally encountered.

The potentially large seed-bank of the species may offset the loss of seed to nonreproductive individuals. Large patches of annual Astragalus have been observed occupying the same sites for several sequential years, without any large input of seeds during that time. Conversely, locations where large, prolific biennials were observed have been revisited in subsequent years without finding any progeny.

Conservation

The more common and wider-ranging var. diaphanus is not in need of any legal protection at this time. The variety has a large range and enough populations to buffer it from loss of individual populations. It would be desirable to monitor populations for long-term demographic trends. Few populations were seen which were threatened by human-related activities.

The plants along the South Fork of the John Day River, var. diurnus, have a very limited range and are represented by few populations. Much of the potential habitat is located on private land and was not searched during my study. All of the sites are subject to livestock grazing, although this does not appear to pose a significant threat. However, cattle are trailed through the Johnson Creek site, which is the largest known population of var. diurnus. The South Fork area is an important wintering ground for big game, and many of the plants at Johnson Creek are grazed by deer in the winter. Off-road vehicle use has occurred at the Johnson Creek site, resulting in direct damage to Astragalus individuals.

The viability of populations at Brown Creek, SFJDR road junction Y and Oliver Creek appears to be tenuous. Each population has only been represented by a few plants, and at the first two localities plants were only found once.

I think that if left alone var. diurnus would continue to exist, but would never be common. Considering the direct and indirect impacts caused by humans, however, I recommend that the variety be given legal protection as an endangered species. Several populations are located on U.S. Bureau of Land Management (BLM) land. A survey of Oregon Department of Fish and Wildlife lands (the Murderer's Creek Wildlife Management Area) might identify new populations on state land. The BLM should develop a management plan to enhance and to avoid detrimental impacts to the habitat of var. diurnus.

Conclusion

In summary, Astragalus diaphanus has a greater range and occurs more frequently than was previously known, although it is not common. There is not a gradation in morphology in the pod, but rather a distinct difference which corresponds to a geographic discontinuity in the distribution. For these reasons I believe it is valid to recognize two varieties. This is also consistent with other treatments which recognize geographic races as varieties.

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APPENDICES

Collections Examined

Astragalus diaphanus Douglas ex Hook. var. *diaphanus*. OREGON: Wasco Co.: 10 mi above The Dalles, 18 June 1921, *Peck 13754* (UC, DS, WILLU); 1 mi E of The Dalles, 28 May 1927, *Peck 14880* (WILLU); 6 mi E of The Dalles, 25 March 1926, *Peck 14565* (DS, WILLU). Sherman Co.: Basalt mosaic flats overlying sand, Columbia River at mouth of John Day River, alt 200 psm, 18 June 1951, *Ripley* & *Barneby 10810* (RSA). Wheeler Co.: Spring Basin, 8 km S of Clarno T8S, R19E, Sec 23 SESE, 7 May 1983, *Wright 1675* (OSC); Sandy washes about 19 mi S of Fossil, 27 May 1962, *Hitchcock* & *Muhlick 22272* (DS, NY); Hilltops above the John Day River 4 mi SE of Spray, T9S, R25E, 2000 ft, 13 May 1950, *Cronquist 6319* (WS); Basaltic rocks above the John Day River 13 mi W of Spray, T9S, R23E, 1700 ft, 27 May 1950, *Cronquist 6435* (RSA, WS, WTU, NY); Sandy soil in wash 2 mi E of Service Creek along the John Day River, 26 May 1950, *Hitchcock 19235* (UC, RSA, WS, DS, CAS, WTU, NY); Basalt slopes above John Day River, 2 mi E of Service Ck, 1700 ft, T9S, R23E, Sec 9 NE, 1 May 1983, *Wright 1674* (OSC); 17 June 1983, *Wright 1688* (OSC); John Day River, 7.7 mi E of Service Ck. 1800 ft, T9S, R24E, Sec 5, 17 June 1983, *Wright 1689* (OSC); 28 May 1984, *Wright* & *Gross 1724* (OSC); 2.8 mi S of Spray along Parrish Ck, T9S, R24E, Sec 11, 650 m, 11 May 1986, *Wright* & *Gross 1810* (OSC). Grant Co.: Hills of Squaw Creek near Humphrey's Ranch, John Day Valley, 22 June 1925, Henderson 5373 (DS, CAS, ORE, GH); Near Humphrey's Ranch along John Day River, T11S, R25E, Sec 30, 680 m, 30 May 1983, Wright 1687 (OSC); 6 May 1984, Wright & Gross 1715 (OSC); Gorge of John Day River, NW of Dayville, sandy streambed alt 2000 psm, 6 June 1945, Ripley & Barneby 6625 (RSA); Middle Fork John Day River, gravel pit E of Ritter, T8S, R30E, Sec 14, 2750 ft, 18 June 1983, Wright 1692 (OSC); About 5 mi W of Ritter, ridgetop above 6 Mile Ck, 3050 ft, T8S, R29E, Sec 10, 18 June 1983, Wright 1693 (OSC); 27 May 1984, Wright & Gross 1722 (OSC); 8 Mile Ck, Middle Fork John Day River, 2900 ft, T8S, R29E, Sec 1, 18 June 1983, Wright 1694 (OSC); Middle Fork John Day River drainage W of Ritter, 3650 ft, T7S, R29E, Sec 26, 18 June 1983, Wright 1695 (OSC); N Fork John Day River, Wrightman Canyon, 2800 ft, T7S, R29E, Sec 17 NWNW, 18 June 1983, Wright 1696 (OSC); Near Devil's Backbone, 5.4 mi E of Wrightman Canyon bridge 2500 ft, T7S, R29E, Sec 3 SE, 18 June 1983, Wright 1697 (OSC); Near Monkey Ck, T7S, R29E, Sec 3, 27 May 1984, Wright & Gross 1719 (OSC); Near Schoolcraft Ck, 9.6 mi E of Wrightman Canyon bridge, 2550 ft, T7S, R30E Sec 4 or 5, 18 June 1983, Wright 1698 (OSC). Umatilla Co.: S facing bank above the N Fork John Day River 4.5 mi E of Hwy 395, T6S, R32E, Sec 29 SE, 19 June 1983, Wright 1699 (OSC); 26 May 1984, Wright & Gross 1716 (OSC). County unknown: Abundantly on the gravelly or rocky banks of the Columbia, Douglas (K!, GH!, isotype); Scot's Bridge, John Day River, May 1882, Howell & Howell s.n. (GH!, holotype of *A. drepanolobus*); On gravel bars, John Day River near its mouth, 10 May 1882, *Howell 44* (DS, WTU, ORE, NY) (considered isotypes of *A. drepanolobus*); John Day River, 15 (19?) May 1885, *Howell* (OSC!, holotype, POM!, NY!, isotypes of *A. craigii*). WASHINGTON: Klickitat Co.: On gravel by the railroad, E of Bingen, 29 April 1914, *Suksdorf 7726* (NY, WS, GH); Railroad, Bingen, 5 May 1920, *Suksdorf 10408* (WS).

Astragalus diaphanus Douglas ex Hook. var. *diurnus* (Wats.) Barneby in Peck. OREGON: Grant Co.: John Day River at Dayville, 19 May 1885, *Howell 383* (GH!, holotype, ORE!, NY!, CAS!, isotypes); S Fork John Day River N of Jackass Ck, 2900 ft, T14S, R26E, Sec 13 NWSW, 4 June 1981, *Wright 1510* (OSC); 29 May 1983, *Wright 1681* (OSC); S Fk John Day River near Johnson Ck, 2700 ft, T13S, R26E, Sec 24, 29 May 1983, *Wright 1677* (OSC); 6 May 1984, *Wright* & *Gross 1714* (OSC); S Fk John Day River above fork in road, 2850 ft, T14S, R26E, Sec 12 SESW, 29 May 1983, *Wright 1682* (OSC); S Fk John Day River above Oliver Ck, 3000 ft, T14S, R26E, Sec 1 NE, 29 May 1983, *Wright 1683* (OSC); S Fk John Day River just N of Oliver Ck, 2900 ft, T13S, R26E, Sec 36 NESW, 30 May 1983, *Wright 1686* (OSC); S Fk John Day River, S of Rockpile Ranch near Magic Lantern, T15S, R26E, Sec 24, 28 May 1984, *Wright* & *Gross 1726* (OSC).

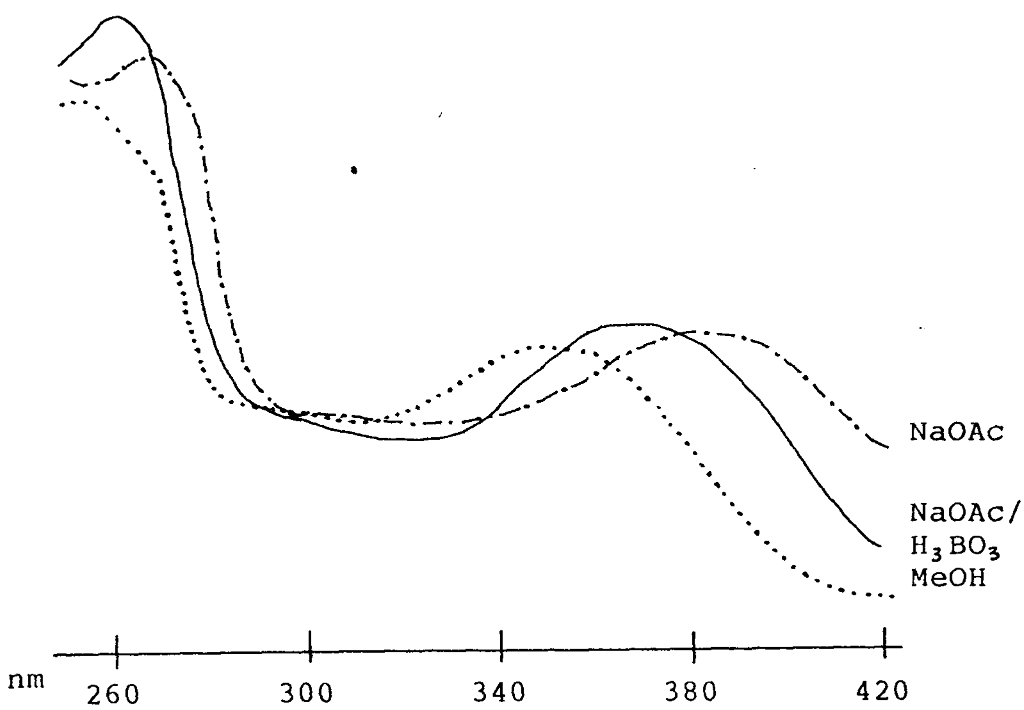
Astragalus sparsiflorus Gray var. majusculus Gray. COLORADO: Park Co.: N Fork, S Platte River 3 mi E of Shawnee, alt 7950 psm, 13 July 1950, Ripley & Barneby 10455 (RSA, CAS, NY); N Fork, S Platte River near Grant, 8810(?) psm, 13 July 1950, Ripley & Barneby 10459 (RSA); Rocky slope near summit of grade E of Bailey, 24 July 1954, Weber & Grant 8801 (COLO); Valley of Platte River just W of Bailey and E of Shawnee, 22 June 1980, Weber & Wittmann 15868A (COLO). Jefferson Co.: Rocky Pinus ponderosa slope along S Platte River just downstream from S Platte Village, 25 June 1983, Weber, Wingate, & Stevenson 16739 (COLO); Platte River Canyon near Waterton, 13 May 1956, Brunquist (COLO). County unknown: On low mountains, rare, 1862, Hall & Harbour 129 (GH!, holotype, NY!, isotype); Along the Platte River, Denver, alt 5300 ft, 12 June 1878, Jones 850 (UTC, POM, DS, COLO); Denver, June 1887, Eastwood (COLO); July 1892, Eastwood (WS); Along railroad, Platte Canon, 19 May 1894, collector unk. (NY); Mouth of Platte Canon, May 1894, (NY); Platte Canon, 19 May 1894 (Crandall) 15 (NY); Mountains of Colorado, August 1891 (1841?), (NY).

Astragalus sparsiflorus Gray var. sparsiflorus. COLORADO: Fremont Co.: Oak Creek Canon, 1 July 1873, Brandegee 562 (UC, NY); Along road between Canon City and Guffey, 12 July 1941, William & Penland 1693 (CAS). El Paso Co.: Pike's Peak region: Ute Pass Trail near Long's Ranch, alt 6000 ft, 27 July 1920, Johnston 2535 (UC, POM); 17 June 1920

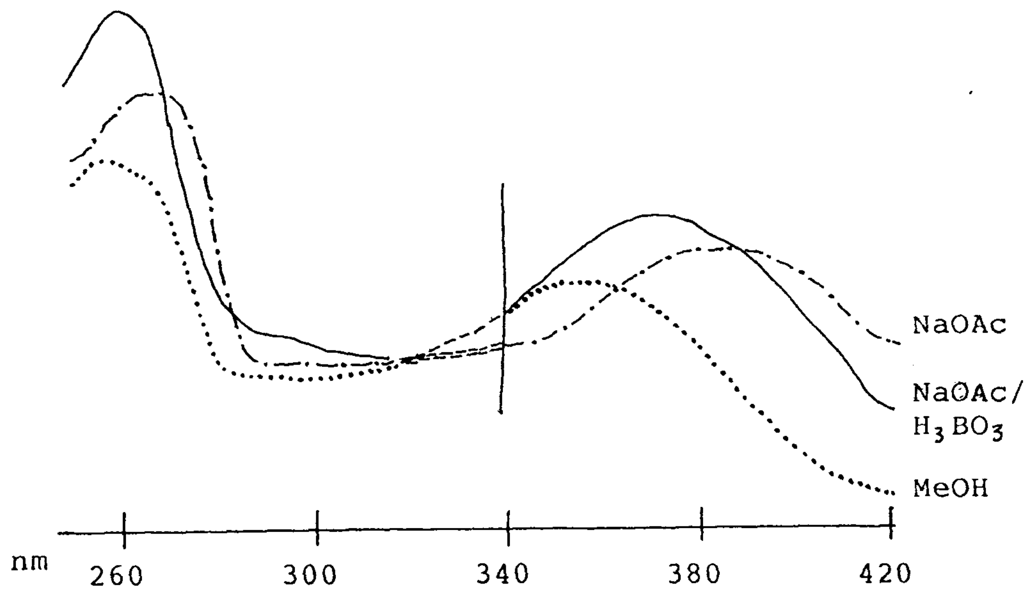
Johnston 2521 (UC); Manitou, 6000ft, 11 August 1883, Woodward s.n. (GH); Manitou, 2100 m, 10 August 1903, Clements & Clements 54.2 (GH); Pikes Peak, cog railroad route between Mountainview and Minnihaha, 6 July 1967, Weber 13294 (GH). Park Co.: N Fork, S Platte River, 3 mi E of Shawnee, steep sunny bank, 7950 psm, 13 July 1950, Ripley & Barneby 10454 (RSA, CAS); Yucca hillside, rocky slope, near summit of grade E of Bailey, 24 July 1954, Weber & Grant 8802 (COLO); Valley of Platte River just W of Bailey and just E of Shawnee, 22 June 1980, Weber & Wittmann 15868 (COLO). Teller Co.: Cripple Creek, 8 July 1910, Treakle (POM). County unknown: On low mountains, rare (also as Rocky Mountains), 1862, Hall & Harbour 128 (GH!, holotype, NY!, isotype); 25 miles below Manitou, alt 6000 ft, 28 May 1878, Jones 126 (UTC, POM, NY); Along the Platte River, Denver, alt 5300 ft, 12 June 1878, Jones 850 (POM); Colorado, Brandegee s.n. (DS); Manitou, 21 May 1879, Jones s.n. (DS); Mountains of Colorado, August 1841,(NY); Mountains of Colorado, August 1871, Canby s.n. (GH); South Park, August 1871, Meehan s.n. (NY); Colorado, 1875, Wilson 107 (NY); Cascade Canon, 8000 ft, 12 July 1895, Bessey s.n. (NY); Near Florissant, alt about 2400 m, 1-8 August 1905, Ramaley 1378 (COLO).

Astragalus wetherillii Jones. COLORADO: Garfield Co.: W facing slope, dry soil, 5 mi N of Rifle along Government Creek, alt 5800 ft, 17 May 1947, Weber 3326 (UTC, RSA, WS, DS, CAS, WTU, COLO); S facing clay slope about 5 mi W of Rifle, along U.S. Hwy 6, 14 June 1967, Welsh & Higgins 6235 (UC, BRY, NY, COLO); Sandy clay on W facing slope about 5 mi S of Rio Blanco Co line along Colo Hwy 789, 13 June 1967, Welsh & Higgins 6228 (BRY, NY); 4 mi N of Rifle on Hwy 789, sandstone slopes and purple mudstone, 2 May 1982, Neese 11278 (BRY, NY); On a loose, well-drained slope 3.9 mi N of Rifle, 3 June 1958, Raven 13057 (CAS, NY). Mesa Co.: Grand River near Grand Junction, May 1892, Eastwood 12 (POM!, holotype, GH!, UC!, CAS!, NY!, isotypes); Talus under sandstone cliffs, Grand River canyon 7 mi below DeBeque, 4800 psm, 17 May 1955, Barneby 12741 (RSA, CAS, NY); Cameo (?) E of Grand Junction, clay bank under cliffs, 4800 psm, 25 May 1943, Ripley & Barneby 5427 (RSA). Montrose Co.: Sandy soil near drainage, Gunnison River Gorge, down Upper Duncan Trail, 6000 ft alt, 16 June 1979, Ratzloff 1649 (COLO). Moffat Co.: Little Juniper Mtn T6N, R94W, Sec 18 NWSE, N side of Juniper Canyon next to river, E of Maybell Ditch, streamside, 14 June 1979, Marv 94 (COLO).

Flavonoid Spectral Scans



Spectral scan of SFJDR-3-slow



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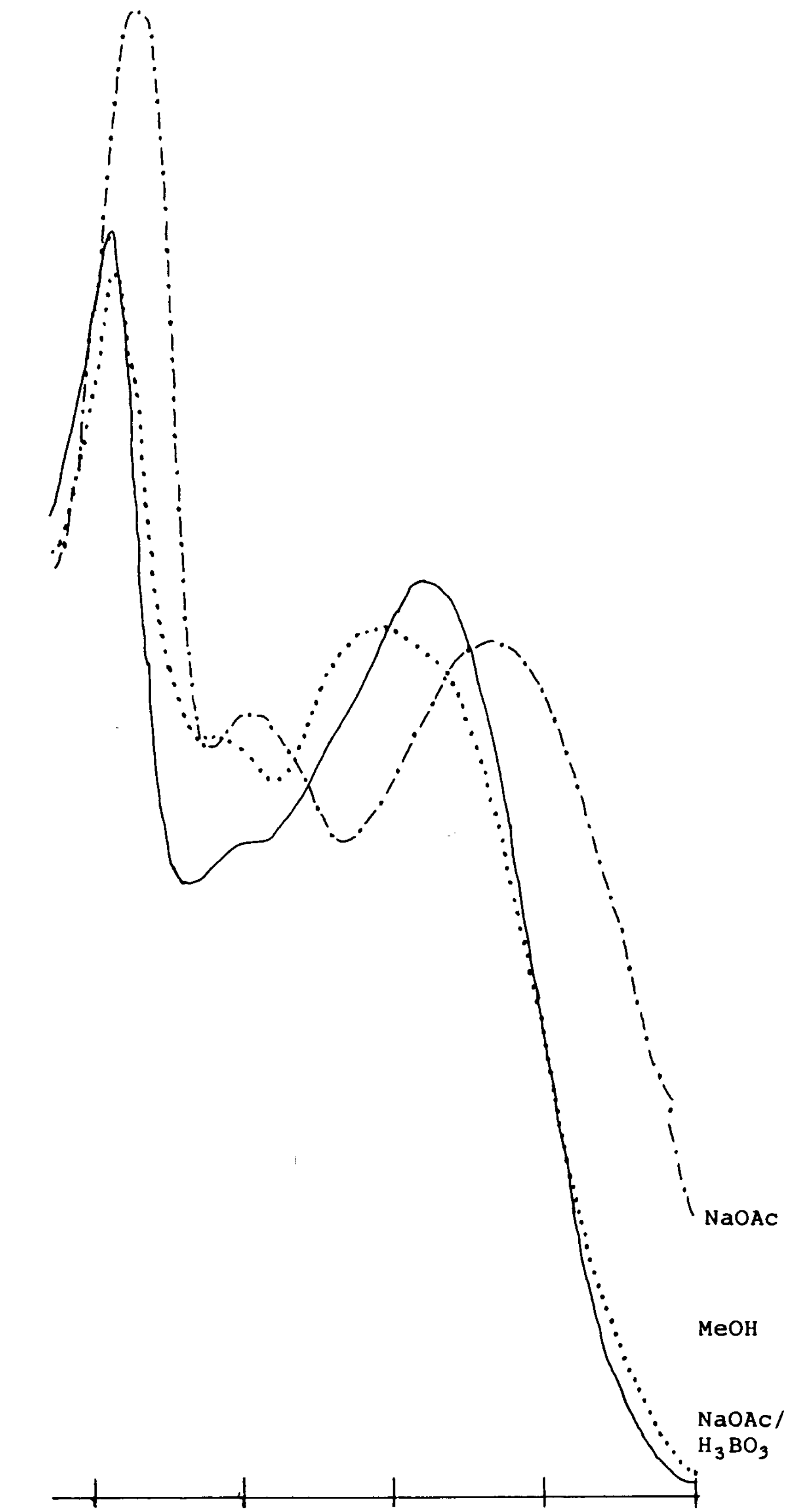

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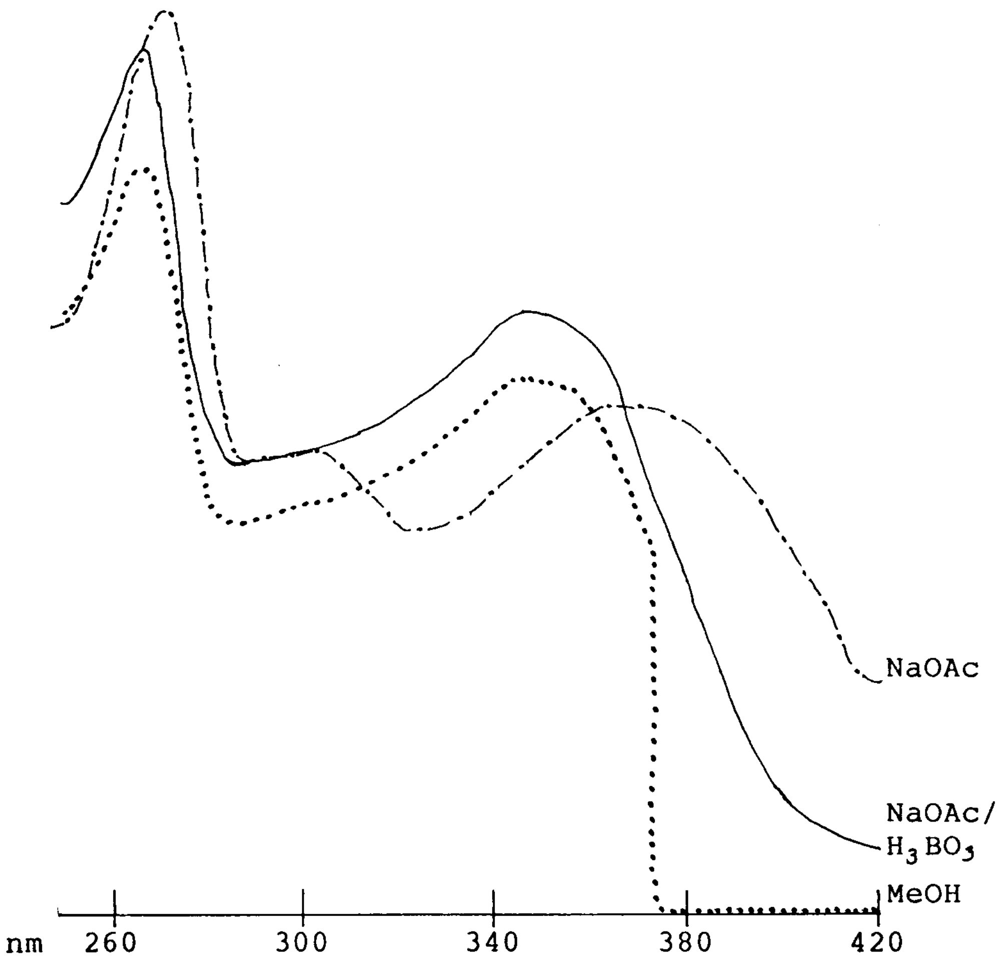

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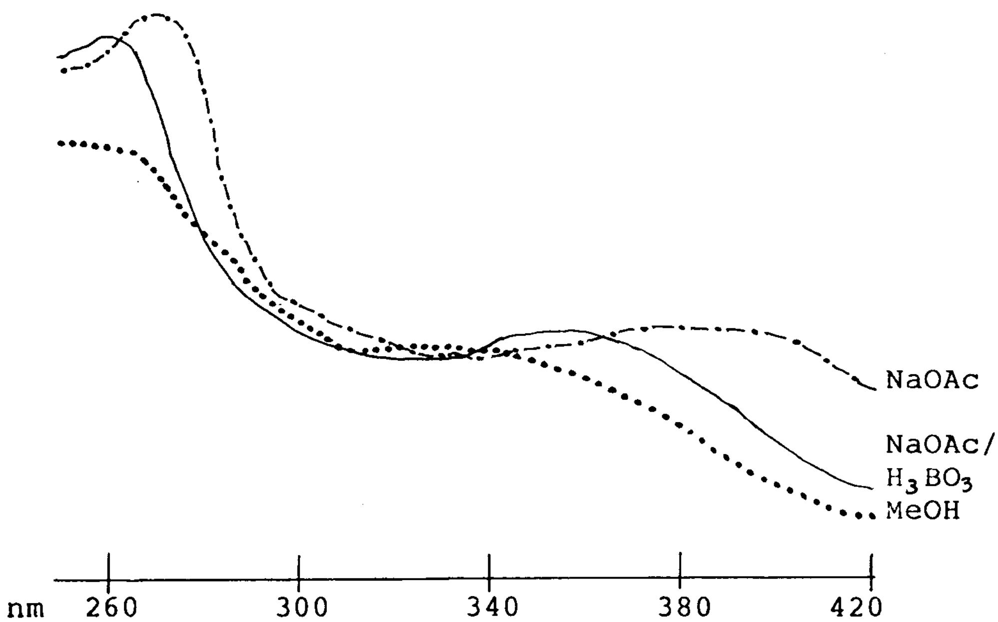
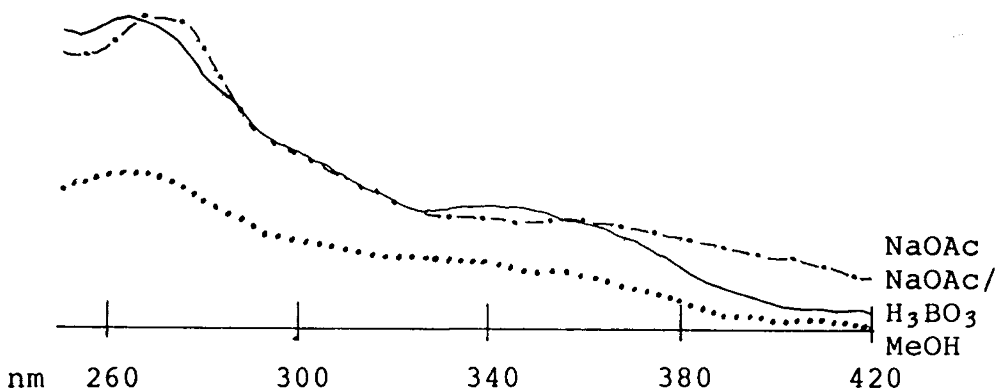
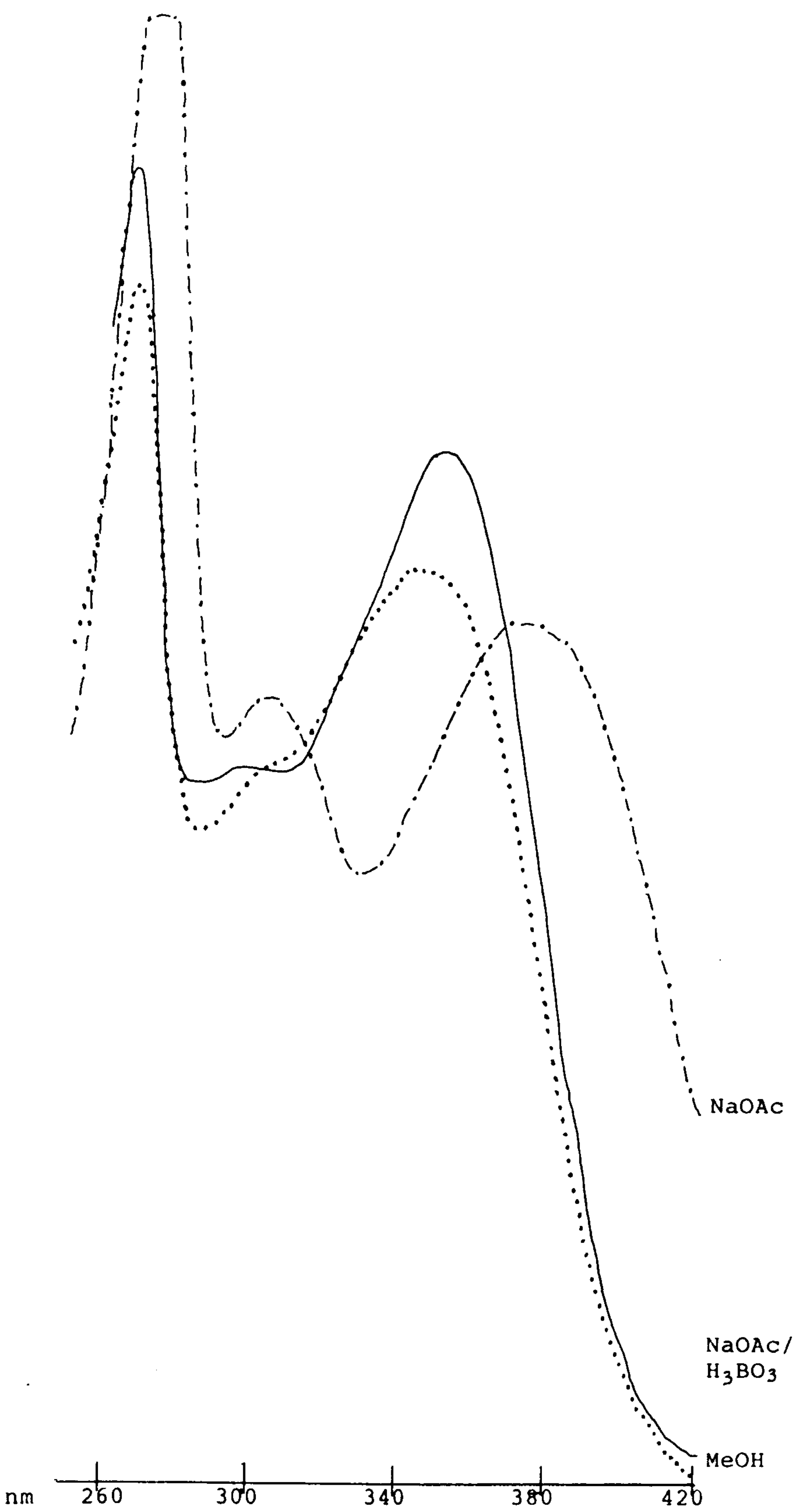


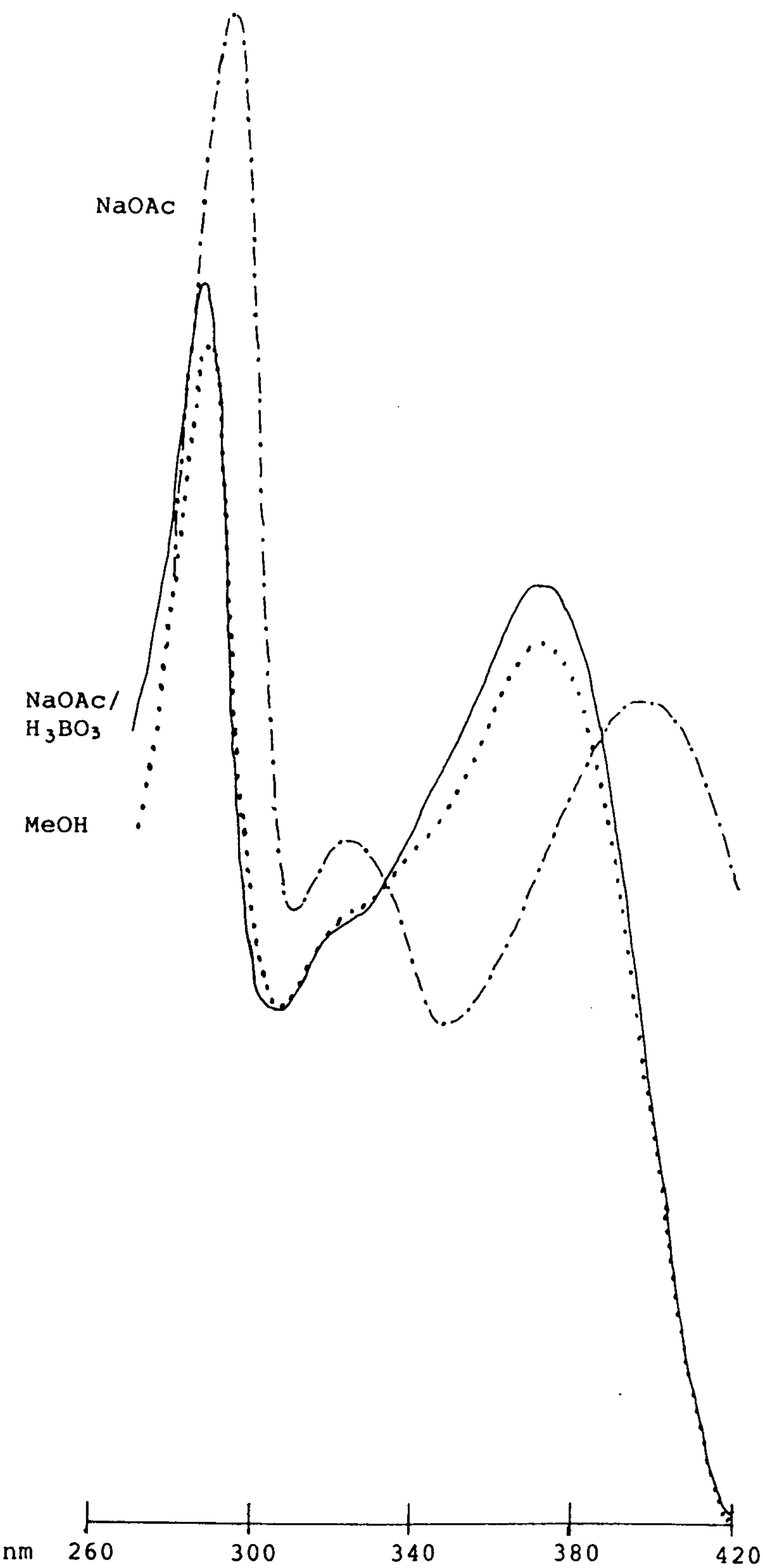
Spectral scan of JDR-5-slow



Spectral scan of JDR-6



Spectral scan of SFJDR-5-med.



Spectral scan of JDR-5-med.